SEASONAL AND DIURNAL PATTERNS OF SPATIAL SPREAD, GROUPING DYNAMICS AND INFLUENCE OF RESOURCES ON A FREE-RANGING CATTLE HERD IN A SEMI-ARID RANGELAND IN SOUTH TEXAS, USA

A Dissertation

by

CHRISTOPHER ELIAS CHELEUITTE-NIEVES

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2011

Major Subject: Rangeland Ecology and Management

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ABSTRACT

Seasonal and Diurnal Patterns of Spatial Spread, Grouping Dynamics and Influence of Resources on a Free-Ranging Cattle Herd in a Semi-Arid Rangeland in South Texas, USA. (August 2011)

Christopher Elías Cheleuitte-Nieves, B.S., University of Puerto Rico-Río Piedras

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Knowledge of scale-dependent factors that affect the distribution of ungulate herds, such as cattle, is essential for the development of more accurate predictive models of animal movement and the management of sustainable agriculture. Our objectives were to evaluate the seasonal and diurnal patterns of herd spread, explore grouping dynamics, and the influence of dominance ranks, seasonal changes in forage biomass, use of shade, water and supplemental feed areas on cattle distribution. Positional and activity information of eleven free-ranging Bonsmara, *Bos taurus*, cows were obtained at five minute intervals using Global Positioning System collars. We conducted a total of 12 trials each of three weeks from August 2007 to August 2009 in a 457ha shrub-dominated savanna in South Texas. Spread was obtained by calculating the average Euclidean distance of individuals to the center of the herd. The association software package, ASSOC1, was used to analyze spatio-temporal interactions. Normalized Difference Vegetation Index, an indicator of available forage biomass, was calculated using satellite imagery. Number of GPS fixes was used as an indicator of animal use of shade patches and water and supplemental feeding areas.

In this semi-arid environment, herd spread was greatest and subgroup division occurred during summer when forage biomass was high. Herd spread was the least and

shade patches were used more during winter when forage biomass was low. Throughout the year spread was smallest and use of shade patches highest during the midday period compared to other periods of the day. Location of individuals in the center of the herd was not associated with their dominance ranking. There was no significant overall pattern of seasonal changes in cattle use of water and supplemental feeding areas.

Seasonal forage availability and shade patches seem to have a greater influence on herd dispersion patterns and grouping dynamics than any effect of social dominance. Herd distribution is likely related to changes in forage biomass and temperature fluctuations which drive compensatory night-time feeding and thermoregulatory actions. Accurate ethological studies of herds depend on our ability to understand herd dynamics at multiple scales that affect and are relevant to animal's response to the landscape.

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1. INTRODUCTION

The need for more accurate and explicit studies of the factors that affect the behavior and distribution of species has increased due to the current critical status of habitat degradation, species invasions, climate change and globalized agriculture (Ritchie et al. 2009; Butt 2010). In particular, ungulates play important roles both in natural environments where they shape the vegetation composition and structure and influence ecosystem function and in managed settings where they provide resources to human populations (Butt 2010; Goheen et al. 2010). Thus, increasing our knowledge of ungulate response to the environment is essential to develop better predictive models of the relationship between animal behavior, ecosystem change and pastoralist livestock operations (Butt 2010).

Foraging behavior of ungulates is influenced by processes that occur at different spatio-temporal scales (Peters et al. 2004, 2006). In turn, these processes might interact and affect animal response to environmental fluctuations and landscape characteristics. Flexible and opportunistic nutritional and physiological responses to the environment develop from this spatio-temporal variability to influence foraging movements both in wild ungulates (e.g. deer) and livestock (e.g. cattle, goats, sheep) as well as in natural and managed settings (Scoones 1995; Parker et al. 2009). This particular relationship between the interaction of environmental variables and ungulate behavior is especially evident in dry environments where sporadic and erratic precipitation leads to a sharp increase in forage production that is not equally distributed throughout the pasture (Sowell et al. 1999). Ungulates possess an accurate spatial memory and are able to associate resources with locations, and thus select nutrient rich areas and avoid nutrient poor areas (Bailey 1995).

This dissertation follows the style of *Animal Behaviour*.

As a consequence, animals will tend to congregate in areas where the required resources are available (e.g. forage, water, minerals, shade) which, in most cases, is not evenly distributed throughout the area (Dudzinski et al. 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; Howery et al. 1996; DelCurto et al. 2000; Ganskopp 2001; Cooper et al. 2008). In arid rangelands, the most abundant and palatable forages often grow in close proximity to water, consequently attracting ungulates to utilize such areas (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005). Cattle movement, for example, is affected by both natural and manmade features such as terrain, aspect, slope, climate, wind (direction), fencing and roads (Hinch et al. 1982; Owens et al. 1991; Bailey 1995; Ganskopp 2001; Harris et al. 2002; Bailey 2004, 2005). In addition to these biophysical attributes of the landscape, cattle distribution is also influenced by management practices. Strategic placement of water, supplemental feed, and salt sources are the management techniques frequently used to alter the distribution of cattle within large pastures. It is less commonly considered that, strong social associations between individuals might influence the distribution of individual animals (Launchbaugh & Howery 2005). Although the nature of these social associations is not fully understood, they could have direct influence on the evenness of pasture use, because strong cohesion might limit exploration of unused pastures by individual animals. Consequently, a few studies have focused on the relationship between cattle distribution patterns and the manipulation of social hierarchies, herd membership and selection of specific breeds (Harris et al. 2002; Bailey 2004).

From a management perspective, grazing ungulates in arid and semi-arid rangelands exhibit uneven grazing distribution pattern where animals select areas of highly palatable forage and in close proximity to water (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005). Consequently, the management goal is to achieve more homogeneous use of the pastures and in doing so decrease over use of the vegetation and possible soil erosion

and increase herd productivity. Grazing selectivity leads to reduction in economic returns and increment of supplemental feed costs, thus threatening the profitability of the livestock industry. Accurate information and knowledge of the factors and interactions that affect livestock movement is necessary to develop more informed management techniques aimed for a better grazing distribution.

From a systems perspective, there is evidence of a complex relationship between resource dynamics, landscape configuration and spatial associations among herd livestock where changes in resource availability and distribution interact and influence the movement of animals (Hinch et al. 1982; Owens et al. 1991; Bailey 1995; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Harris et al. 2002; Bailey 2004, 2005; Launchbaugh & Howery 2005). Two important and essential steps towards more accurate ethological studies of herd dynamics are to 1) use multiple spatio-temporal scales to understand how scale-dependent processes affect the behavior of the animal and how these processes interact and influence animal response and 2) focus analysis efforts at the spatial and temporal scales that are relevant to animal's response to the landscape rather than that of the investigator. Some of the processes that occur at different scales might be interacting to influence the ecosystem and affect the behavior of the animals in ways that are distinct from the effects of single scale processes alone (Peters et al. 2004, 2006). This results in a cross-scale interaction of system processes that might provide novel insight about the factors and relationships that affect animal movement dynamics. Furthermore, same or similar species might behave differently depending on the landscape configuration and environmental conditions of an area. The inherent flexibility of animal responses to change imply that ethological studies that focus in only a few ecological areas or at a particular time of the year might lead to erroneous conclusions or omit parts of the entire behavioral spectrum. For that reason it is necessary to study organisms under different settings of topography and climate regime. Technological advances in spatio-temporal data acquisition can allow for such type of multi-scale analysis

and may shed light into the influential ability of fine-scale processes to broader scales processes and vice versa.

Cattle with limited management interferences are a good model for empirical testing of large herbivore herd movement patterns (Reinhardt 1982; Šárová et al. 2010) because they can behave without restrictions and with minimal human influence like natural, wild herds while allowing for ease of handling (Reinhardt 1982). Livestock distribution studies were usually based on field observations of a few animals and the social influence and associations between cows in close proximity were difficult to measure (Stricklin 1983; Turner et al. 2000, 2001; Harris et al. 2007). These studies had limited accuracy, few to no replications, and almost no night observations. Global positioning systems (GPS), integrated with geographical information systems (GIS) provide the ability to capture the spatial interactions among members of a herd in much greater than previously used methods (Ganskopp et al. 2000; Ungar et al. 2005). These technologies provide accurate location of individuals making it is possible to relate this spatial information to environmental variables, landscape attributes, and social interactions (Ungar et al. 2005).

Three sections of this dissertation address topics related to cattle herd movement dynamics in the shrub-dominated semi-arid rangelands of the Southern Plains of North America and the environmental and social factors that might influence herd distribution at the diurnal and seasonal scale using explicit spatio-temporal data from GPS collars. The objective of the first section was to determine cattle activity using motion sensor data from GPS collars and to determine the seasonal and diurnal dynamics of herd spread (e.g. degree of dispersion) and its relationship to activity (e.g. grazing, traveling, resting) schedules. Previous studies have concluded that slope, distance to water, and forage characteristics are the major factors influencing cattle distribution (Friend & Polan 1974; Arave & Albright 1981; Stricklin 1983; Grant & Albright 2001; Harris et al. 2007). Although these studies have explored important abiotic (e.g. slope, distance to water) and biotic (e.g. animal

breed, forage abundance and quality) factors that influence cattle movement, they mostly focused their analysis using one temporal scale (e.g. seasons) and have been conducted in north-western mountainous rangelands where slope and wind are major factors influencing cattle distribution. The Southern Plains, however, has gentle terrain and very different temperature, precipitation and vegetation production regimes from those in the Northwest. Arid and semi-arid rangelands are particularly subject to uneven cattle grazing distribution patterns due to extreme environmental conditions (e.g. high temperatures, low precipitation) and limited forage production and water availability. Thus, it is essential to conduct explicit and accurate analyses of cattle herd movement patterns in such dry environments to gain a better understanding of the underlying factors that influence their behavior and how they related to each other.

The objective of the second section was to determine the spatio-temporal parameters that characterize a cattle herd using GPS technology, to explore possible formation of sub-herds using association techniques and to determine the relationship between herd membership, spatial associations and dominance ranks. Determining the spatio-temporal relationships among individuals within groups can help to better understand the spatial and social structure of a herd such as subgroup membership and dominance hierarchy (Lazo 1994; Harris et al. 2007). Although previous studies have addressed some questions regarding the relationship between spatial interactions and social interactions in a cattle herd, they do not fully examine the explicit spatial, temporal and social dominance parameters that characterize a herd or sub-herd throughout the year (Friend & Polan 1974; Arave & Albright 1981; Stricklin 1983; Grant & Albright 2001; Harris et al. 2007). A major limiting factor for studying herd systems was stated by Harris et al. (2007) who concluded that defining at what spatial threshold subgroups would be delineated was the main problem during their investigation of cattle subgroup dynamics. Also, social dominance and competition for feed affects the feeding behavior and the spatial relationships among member of the herd and may, in turn, lead to detrimental effects

to subordinate individuals. However, little information is known on how dominance behavior affects group spatial distribution in domesticated animals, such a beef cattle, and how it varies seasonally particularly in a semi-arid rangeland where resources are often limited and erratic (Wagnon et al. 1966). Our study provides specific knowledge of the broader spatial thresholds that define the herd unit and the finer spatial thresholds that detect diurnal and seasonal grouping dynamics and influence of dominance behavior. This knowledge improves our understanding of the spatial perspective under which a cattle herd functions and perceives the landscape and could prove useful in the management of cattle herds and decisions related to herding and selective culling aimed for a more even pasture use.

The objective of the third section is to quantify and compare the influence of the distribution of resources and structures in the landscape (e.g. shade patches, forage production, water and supplemental feed) on the spatial pattern and temporal dynamics of cattle herd distribution. Although previous studies have explored important abiotic (e.g. slope, distance to water) and biotic (e.g. animal breed, forage abundance and quality) factors that influence cattle movement, more information is needed on the explicit spatio-temporal distribution of cattle herds in response to landscape characteristics at both the diurnal and seasonal scale (Dudzinski et al. 1982; Sato 1982; Lazo 1994; Howery et al. 1996; Harris et al. 2002; DelCurto et al. 2005). Most studies have focused on only one temporal scale, but to more accurately capture the entire behavioral spectrum of animals and to develop sound management techniques aimed to promote a more even pasture use it is critical to understand how processes occurring at multiple spatio-temporal scales interact and affect the movement patterns of ungulates. In sum, the information obtained on these three sections should prove useful to better understand cattle herd behavior and use this knowledge to develop better predictive models of animal distribution and improve management techniques aimed to manipulate spatial patterns, enhance animal comfort, increase production efficiency and be more compatible with the behavior of the animals (Stricklin 1983; Bailey 1995; Ritchie et al. 2009).

2. CROSS-SCALE SPATIAL AND TEMPORAL SPREAD AND ACTIVITY PATTERNS OF A FREE-RANGING CATTLE HERD IN A SEMI-ARID RANGELAND

Introduction

Large herbivore movement dynamics, such as those seen in free ranging cattle herds, are influenced by spatial patterns in topography and resource distribution, and temporal patterns in resource availability, resource quality, and environmental fluctuations (Hinch et al. 1982; Owens et al.1991; Bailey et al. 1996; Bailey 1995, 2004, 2005; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Harris et al. 2002; Launchbaugh & Howery 2005; Ritchie et al. 2009). Due to physiological needs and constraints, animals tend to congregate in areas where the required resources are available which, in most cases, are not evenly distributed throughout the landscape (Bailey 1995; Ganskopp 2001). Wild and domestic ungulate herds grazing in arid and semi-arid rangelands exhibit uneven grazing distribution due to the animals' tendency to select areas of highly palatable forage in close proximity to critical resources like water (Belovsky 1984; Senft et al. 1987; Frixell 1991; Ganskopp 2001; Bailey 1995; Scoones 1995; Seagle & McNaughton 1992; Wallace et al. 1995; Cooper et al. 2008; Parker et al. 2009). Particularly in riparian zones, uneven pasture use can result in soil erosion, degradation of vegetation, bacterial contamination of watersheds and damage to threaten and endangered species (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Harris et al. 2007; Butt 2010). However, large herbivore selective grazing patterns are essential in maintaining ecosystem structure and function (Goheen et al. 2010). Accordingly, the activities and spatial distribution of large herbivores are influenced by the environment and spatio-temporal processes occurring at different scales and, in turn, they affect the ecosystem by establishing alternate stable states in the community. Although previous studies have explored important abiotic (e.g. slope, distance to water) and

biotic (e.g. animal species, forage abundance and quality) factors that influence large herbivore movement, the relationship and interaction of processes occurring at different temporal scales in relation to ungulate herd distribution dynamics has not been fully explored (Senft et al. 1987; Bailey et al. 1996; Johnson et al. 2002; Seagle & McNaughton 1992; Weladji et al. 2002; Peters et al. 2004, 2006).. It is necessary to identify scale-specific responses of animals to the environment and their dynamics in association with different activities (e.g. grazing or resting) using multiple temporal scales (e.g. day, season) (Hinch et al. 1982; Owens et al. 1991; Bailey 1995; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Harris et al. 2002; Bailey 2004, 2005; Launchbaugh & Howery 2005). Biological systems are complex and processes occurring at different scales interact to influence the system and, consequently, affect the behavior of the animals in unique ways (Johnson et al. 2002; Peters et al. 2004, 2006). Hence, examination of a multi-scale interaction of system processes might provide novel insight about the factors and relationships that affect animal movement dynamics that can be used to develop better predictive models of animal distribution and their effect on the environment (Bailey 1995; Ritchie et al. 2009).

Cattle with limited management interferences are a good model for empirical testing of large herbivore herd movement patterns (Reinhardt 1982; Šárová et al. 2010) because they can behave without restrictions and with minimal human influence like natural, wild herds while allowing for ease of handling (Reinhardt 1982). Many studies show evidence of complex relationships between resource distribution, resource quantity and quality, landscape configuration and spatial associations among cattle in a herd. Most studies conclude that slope, distance to water, and forage characteristics are the major factors influencing cattle distribution and that the magnitude of the effect varies with the seasons and range site (Hinch et al. 1982; Owens et al. 1991; Bailey 1995, 2004, 2005; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Harris et al. 2002; Launchbaugh & Howery 2005). However, most of these studies were conducted in north-western mountainous

rangelands of North America where slope and wind are major factors influencing cattle distribution. The Southern Plains in North America have gentle terrain and very different temperature, precipitation and vegetation production regimes from those in the Northwest (Taylor et al. 1999). There is also a lack of information on the dynamics of grouping behavior of individuals within the herd and their cross spatial and temporal relationships with their environment. Therefore, further explicit spatio-temporal analyses are needed to better understand the relationships of broad temporal scales (season), fine temporal scales (day), and animal activity and their impact on ungulate herd dispersive patterns. Global positioning systems (GPS), integrated with GIS and remote sensing technologies have been used to understand the relationship between landscape characteristics and animal movement dynamics (Ganskopp et al. 2000; Turner et al. 2000, 2001; Ungar et al. 2005). These advances in spatiotemporal data acquisition enables the effective tracking of animals movements and landscape use which can provide a new body of information useful for more accurate behavioral ecology studies and assessments of ecosystem impact by animals (Ungar et al. 2005).

The goal of this study was to understand the spatial distribution of a cattle herd and the factors and scale dependency influencing herd spread in semi-arid rangelands. The specific objectives were (1) to determine cattle activity and location and (2) to examine the seasonal patterns of herd spread as a function of season, periods of the day and animal activity schedules. The information obtained at multiple temporal scales should provide valuable information about the factors that influence herd spatial distribution and how these relate to each other.

Methods

Study site description

The rangelands of the southern United States are part of the tropical savanna biome, which also include areas of South America, Africa, Australia and India (Ricklefs 2001). The study site was a 457-ha ranch in Uvalde, Texas (lat

29°19’8.584”N, long 99°42’54.161”W), located in the South Texas Plains Ecoregion at the transition zone from the Edwards Plateau. Topography is mostly level with gentle undulating planes (Taylor et al. 1999). Uvalde County has a semi-arid climate characterized by dry winters and hot, humid summers (USDA 1976). Average annual precipitation is 406 mm with substantial inter-annual variations. Over 2/3 (68%) of the precipitation occurs during the warm season from May through October, usually with the highest amount of rainfall in May followed by a second rainfall peak in September. Average temperatures range from 2.9°C in winter to 36.7°C in summer. The growing season lasts 340 to 360 days.

Soils in the west part of the ranch were mostly Montell clay (0 to 3% slope) characterized by gently sloping, deep, calcareous soils formed in clayey alluvium on outwash plains (Clay Flat range site; USDA 1976). Soils in the east part of the ranch were mostly undulating Olmos on low ridges characterized by shallow calcareous soils formed in beds of caliche (Shallow Ridge range site). The ranch was externally fenced and had no natural hydrological sources, but had three water tanks and a large pond on the southeast part of the ranch. There was a network of dirt roads to facilitate cattle and deer management. The property was under a continuous year-long grazing schedule with a stocking rate of 15 ha/AU.

The study area had a 29.4% woody cover composed by low-growing, thorny vegetation that formed dense mottes of small trees and shrubs with a grass matrix. Small trees of live oak, (*Quercus virginiana*), formed mottes scatted throughout the landscape, and these are surrounded by a diverse variety of shrubs. Dominant shrubs were catclaw acacia (*Acacia greggii*), guajillo (*Acacia berlandieri*), Texas persimmon (*Diospyros texana*), agarita (*Mahonia trifoliate*), whitebrush (*Aloysia gratissima*), hogplum (*Colubrina texensis*), guayacan (*Guaiacum angustifolium*), honey mesquite (*Prosopis glandulosa*), twisted acacia (*Acacia schaffneri*), spiny hackberry (*Celtis ehrenbergiana*), and cenizo (*Leucophyllum frutescens*). Succulents like Texas pricklypear (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), and Yucca spp. were also common. Herbaceous species were mostly composed of Halls

panicum, (*Panicum hallii* var. *hallii),* hairy tridens (*Erioneuron pilosum*), common curlymesquite (*Hilaria belangeri*), Texas grama (*Bouteloua rigidiseta*), sideoats grama (*Bouteloua curtipendula* var. *curtipendula*), threeawn (*Aristida* spp.), plains bristlegrass (*Setaria leucopila*), slim tridens (*Triden muticus* var. *muticus*), red grama (*Bouteloua trifida*), and Texas wintergrass (*Nassella leucotricha*). Common forbs included cardinal feather (*Acalypha radians*), Indian mallow (*Abutilon fruticosum*), orange zexmenia (*Wedelia texana*), frostweed (*Verbesina virginica*), ruellia (*Ruellia metzae*), ragweed (*Hymenopappus artemisiifolius* var. *artemisiifoliu,),* silverleaf nightshade (*Solanum elaeagnifolium*), hairy tubetongue (*Justicia pilosella*), cedar sedge (*Carex planostachys*), and prostrate lawnflower (*Calyptocarpus vialis*) (R. Cooper personal observation; TAMU Uvalde Herbarium 2008).

Animal selection and GPS collars

Telemetry collars containing GPS receivers and dual axis activity sensors (Lotek GPS 3300LR; Lotek Engineering, Newmarket, Ontario, Canada) were placed on 11 randomly selected individuals from a single herd of 31 free-ranging Bonsmara cows (*Bos taurus*). The animals were four to six years old during the study period and had an average weight of 1193.2±38.4 kg. Cows were pregnant during the autumn and winter seasons and gave birth at the end of the winter season. A bull was present during late spring and early summer. Supplemental feeding occurred throughout the year (2-3lbs/animal) with higher frequency during the non-growing season. Supplemental feed operations occurred at least three times per week between 10:00 and 15:00 at one location per operation. The supplement consisted in 20% (crude protein) breeder range cubes, which is a feed for mature beef cattle on pasture.

The 11 selected individuals and their respective GPS collars were kept constant throughout the study. Animals were handled according to Texas A&M University Institutional Animal Care and Use Committee Animal Use Protocol # 2007-167. The GPS collars provided information on location, date, time, ambient

temperature, and animal activity on two axes. Location was accurate to within 2m after differential correction (Lotek 2006). The wide range temperature transducer measured and recorded ambient temperature with accuracy of ± 1°C within the operating temperature of the collar. The dual axis motion sensors were sensitive to vertical (fore-aft) and horizontal (left-right) movements of the head and neck and recorded the number of times a switch was triggered during the four minutes preceding a GPS fix (Coulombe et al. 2006). Every five minutes the activity data of both axes were stored on collar's memory. Sensor data also included the percentage of time the Y sensor was in the "down" position.

Sampling period and data processing

The operational schedule for the collars was set for a GPS fix interval of 5 minutes and an activity-sampling period of 4 minutes. Positional and activity data was recorded at synchronized fix intervals for all 11 individuals for 21 days per trial. Predictive models using GPS fix intervals of 5 minutes are more appropriate and effective in determining and separating activities than when using larger fix intervals (Ungar et al. 2005). Turner et al. (2000) reported an increase in error if the GPS fix interval was increased from 5 to 30 min. They suggest that intervals greater than 5 min may not be able to identify certain types of data such as discrete watering events or accurate interpretation of animal activity. Ganskopp (2001), in a study using 20-min resolution, also concluded that to adequately model activities a more frequent sampling interval might be necessary. However, spatial data with successive records separated by short time intervals (e.g. 5 minutes intervals) and the non-random movement of animals can produce autocorrelated points with redundant information that violates statistical independence (Swihart & Slade 1997; de Solla et al. 1999). Preliminary analyses (Perotto-Baldivieso et al. In press) indicates that 120 minutes intervals between GPS fixes can significantly reduce autocorrelation and therefore the data was thinned to 120 minute intervals for our seasonal spread analysis by randomly selecting the first data point and then obtaining the rest of the points using

the appropriate interval length. On the other hand, for our diurnal and activity spread analysis we used a 5-min GPS fix interval to obtain sufficient data for the different time periods and to capture most of the activity events.

Two sampling trials per season (i.e. autumn, winter, spring, summer) were conducted, to account for within season variability, for a total of 8 trials from September 2007 to August 2008 (Table 2.1). At the end of each period all data was retrieved from the collars, differentially corrected using N4 v.1.2138 Differential post-processing software (Lotek 2006) and Del Rio station as the base location (NOAA 2007). When differential corrections were not possible (e.g. no data from base station), an uncorrected position was used. When no collar integration was obtained, series of three consecutive records were interpolated to complete the data set (Ganskopp & Johnson 2007). If more than three successive fixes was not obtained, that portion of the dataset was omitted from analyses.

Table 2.1. Average maximum and minimum temperature and precipitation for each trial. Weather data was collected with the weather station at the Uvalde AgriLife Research Center, TX

Season	Date	Max Temp (C)	Min Temp (C)	Precip (mm)
Early Fall	Sept. 10 - Sept. 24, 2007	32	22.1	0
Late Fall	Oct. 26 - Nov. 16, 2007	26.2	13.3	0
Early Winter	Nov. 29 - Dec. 20, 2007	21.4	8.3	0.2
Late Winter	Jan. 17 - Feb. 7, 2008	17.8	5.7	0.1
Early Spring	Feb. 26 - Mar. 18, 2008	25.1	8.4	0.4
Late Spring	Apr. 30 - May 21, 2008	32.1	18.3	2
Early Summer	Jun. 6 - Jun. 27, 2008	36.2	21.5	0
Late Summer	Aug. 1 - Aug. 22, 2008	35.3	23.3	5.3

Four periods of the day were selected to capture the diurnal variation in animal behavior based on past research (Gary et al. 1967; Stricklin et al. 1976; Scoones 1995; Ganskopp 2001; Parsons et al. 2003). The periods were: (1) early morning (grazing bout): first three hours after sunrise; (2) midday (resting bout):

three hours around the solar noon; (3) late afternoon (grazing bout): last three hours before sunset; and (4) midnight (resting bout): three hours between time opposite of solar noon. Data was processed using ArcView 3.2 and 9.3 (ESRI, Redlands, CA) to convert the differentially corrected data (latitude/longitude form) to Universal Transverse Mercator (UTM 14-N) coordinate system to allow the algebraic derivation of straight-line distances between successive GPS fixes (Ungar et al. 2005).

Animal activity

Field work was conducted to observe the behavior of each collared animal in order to calibrate the activity sensor data, as recommended by Ungar et al. (2005). Observations were made during early morning and late afternoon because those are periods of greater activity variation and shifts (Bailey 1995). Activities recorded were grazing (including walking while grazing as long as the head is down), traveling, and resting (lying and standing). Observational data was later synchronized with the sensor data of each individual for further analyses.

The simultaneous procedure for discrimination analyses proposed by Ungar et al. (2005) was used to infer animal activity. This methodology uses activities divided into three distinct classes: left-right motion sensor count, fore-aft motion sensor count, and the distance between GPS fixes and observed activities. Distance between GPS fixes was calculated using Euclidean distances between UTM coordinates (meters). Distance between successive points (i.e. distance for a traveling individual) was probably underestimated because calculations assume a straight-line travel (Ungar et al. 2005). Significant differences in mean discriminant function scores were identified by use of the Wilks' Lambda (λ) statistic (SPSS Statistics).

Herd spread calculation

To understand cattle grouping behavior and degree of dispersion we obtained the spread by using the distance from the group center (DGC) (Stricklin 1983; Waser

1985; Kunz & Hemelrijk 2003; Wolfram Research 2007). The average distance of all individuals to the center of gravity of the herd for each time interval was used to represent the spread of the herd at that time. The center of gravity of the herd was calculated by averaging the X and Y coordinates of the 11 individuals for each GPS fix. The Euclidean distance from each individual to the center of the herd was then calculated. Spread calculations were summarized to estimate the mean and standard error for all trials. Mean comparisons were conducted to examine the overall seasonal and diurnal patterns of herd spread, as well as the seasonal patterns of herd spread as a function of time of the day and activities. Kruskal-Wallis (H) one-way analysis of variance on ranks Test was used to examine statistical differences in the average spread of the herd between seasons, time periods, and activities.

Results

Classification of animal activities using collar variables

A total of 300 field observations were made. Resting, grazing, and traveling activities accounted for 28%, 48%, and 24% of the observations, respectively. Useful discriminant functions were found for the left-right motion ($\lambda = 0.804$, F = 36.250, $P < 0.0001$), fore-aft motion ($\lambda = 0.909$, $F = 14.814$, $P < 0.0001$), and distance between fixes ($\lambda = 0.501$, $F = 148.113$, $P < 0.0001$). Discriminant analysis of animal activity (grazing, resting, and traveling) based on the collar variables yielded a correct classification rate of 73% ($\lambda = 0.403$, $P < 0.0001$). Specifically, 29% of the resting activity was misclassified as grazing and 22% of the traveling activity was misclassified as grazing (Table 2.2). Based on the small and significant λ values and the plotted activity/collar variables relationships, the distance variable seemed to be the best predictor of animal activity followed by the left-right motion sensor.

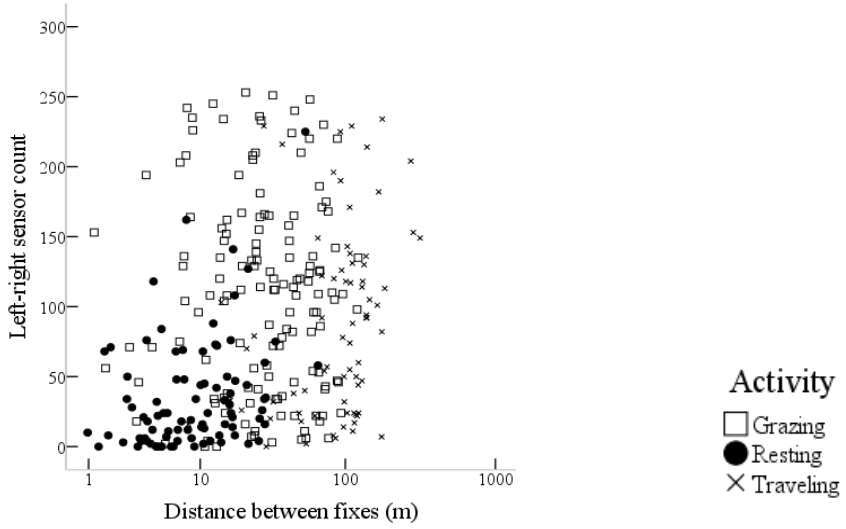
Table 2.2. Frequency count and percent of field observed activities in predicted activity categories based on discriminant analysis.

Observed Activity	**Predicted Activity**			Total Count
	Resting	**Grazing**	**Traveling**	
Resting	60 (70.6%)	25 (29.4%)	0 (0%)	85
Grazing	22 (15.4%)	111 (77.6%)	10 (7%)	14 3
Traveling	9 (12.5%)	16 (22.2%)	47 (65.3%)	72

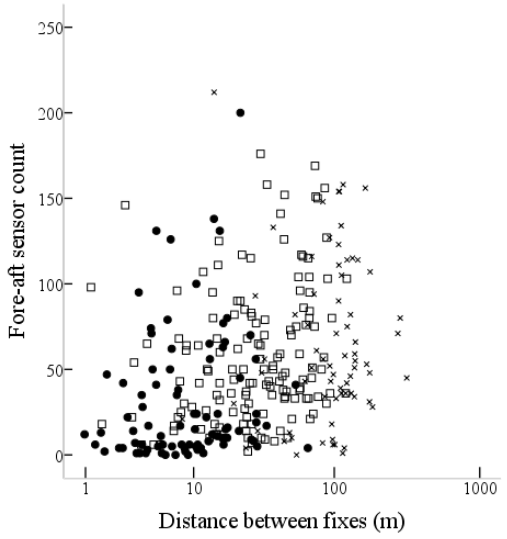
Resting was generally characterized by values less than 100 in the left-right sensor count and less than 30 m in the distance variable. Grazing and traveling appear to be associated with high values (> 100) of the left-right sensor counts. Grazing predominates at intermediate values (10 – 100 m) and traveling at large distance values > 100 m. The distance between GPS fixes variable separated most of the resting and traveling activities when plotted against the other two collar variables: the left-right motion sensor count (Fig. 2.1a) and the fore-aft motion sensor count (Fig. 2.1b). Using the relationship between the left-right and fore-aft sensor counts alone did not strongly separated any of the activities (Fig. 2.1c). Results from the relationship of the three collar variables and activities showed that some areas of the response space were occupied by a single activity; however there were also regions in which activities overlap thus a potential source of misclassification for the discriminant analysis.

The discriminant function was applied to the entire dataset to obtain the overall herd activity during each trial. The overall herd activity was decided when seven or individuals were performing the same activity. This analysis revealed that resting had the highest frequency for all trials, followed by the grazing activity (Fig. 2.2). The traveling activity had the lowest frequency for all trials.

a)



b)



c)

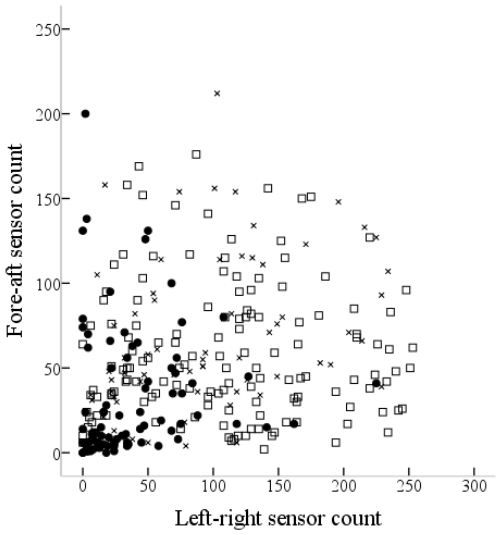


Figure 2.1. Relationship between GPS collar variables and cattle activities: grazing, resting and traveling for Bonsmara cows in South Texas. The graphs show the relationship of distance between GPS fixes and left-right sensor count (a), fore-aft sensor count (b), and the relationship between fore-aft and left-right sensor counts (c).

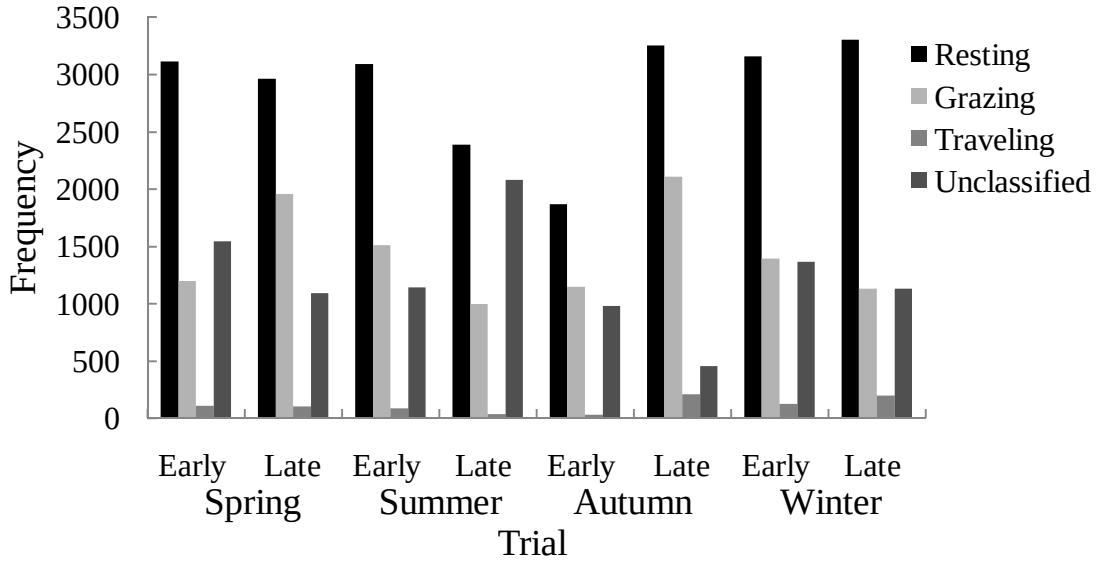


Figure 2.2. Frequency of the overall herd activity per season of a free-ranging cattle herd (N = 11) during eight trials of three weeks from Sept. 2007 to Aug. 2008.

Herd spread

Herd spread varied seasonally and was significantly greater during summer and autumn and least during winter (H_3 = 176.19, P < 0.001; Fig. 2.3). Herd spread ranged from X +SE = 181.01+9.44 m, N = 492 in winter to X +SE = 337.73+12.10 m, N = 442 in summer. From spring to summer there was a significant increase in the spread of the herd. This was followed by a small and non-significant decline in autumn and then a large and significant reduction in herd spread during winter.

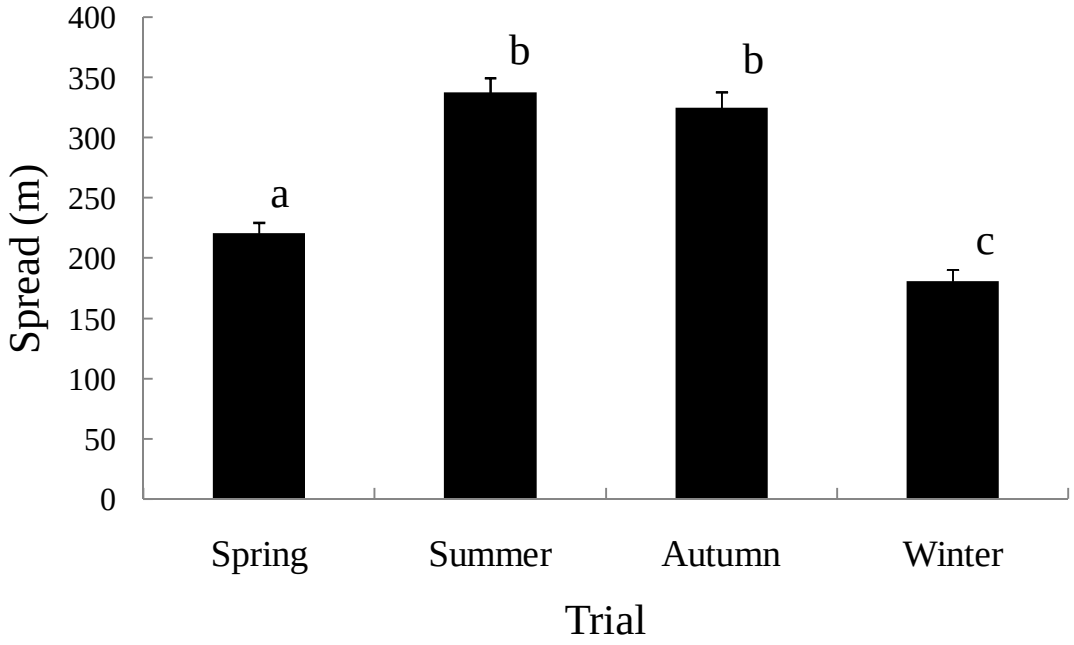


Figure 2.3. Mean and standard error of the spread per season of a free-ranging cattle herd (N = 11) during four trials of three weeks from Sept. 2007 to Aug. 2008. Different letters indicate significant difference ($P < 0.01$).

Herd spread also varied by time of day, overall, herd spread was significantly smaller in the midday period ($X + SE$ = 225.35+3.24 m, N = 5,569) than compared to the other measured time periods (H_3 = 510.57, $P < 0.001$, Fig. 2.4). Early morning, late afternoon, and midnight periods showed very similar mean spread ($X + SE$ = 271.75+3.23 m, N = 5,569). Diurnal patterns of herd spread also changed between seasons. Seasonality of herd spread at different times of the day is shown in Figure 2.5. During the summer, the herd had greatest spread in the early morning and during winter the herd had greatest spread during around midnight.

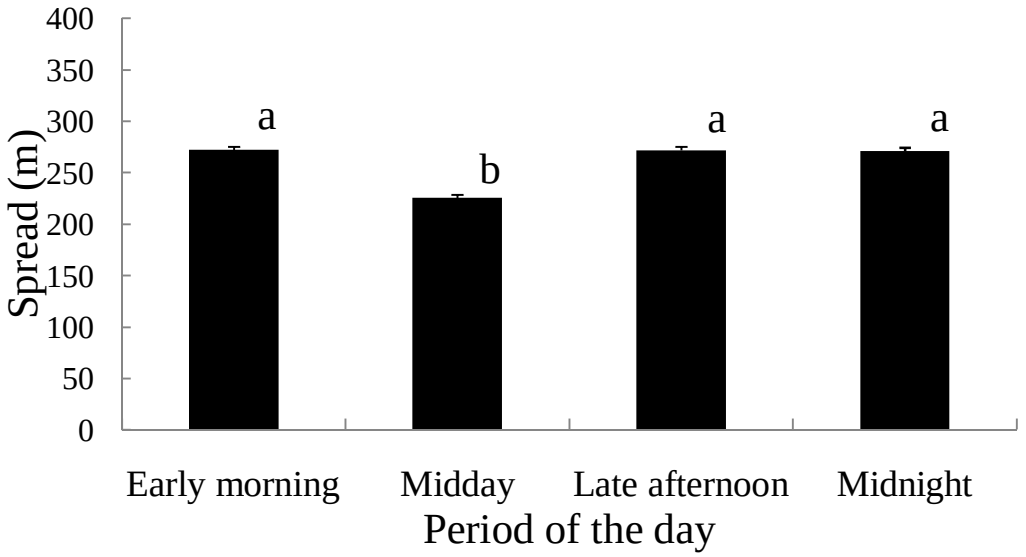


Figure 2.4. Mean and standard error of the spread per period of the day with all trials combined of a free-ranging cattle herd (N = 11) during eight trials of three weeks from Sept. 2007 to Aug. 2008. Different letters indicate significant difference ($P < 0.01$). Periods of the day were selected as: (1) Early morning: first three hours after sunrise; (2) Midday: three hours around solar noon; (3) Late afternoon: last three hours before sunset; and (4) Midnight: three hours opposite of solar noon.

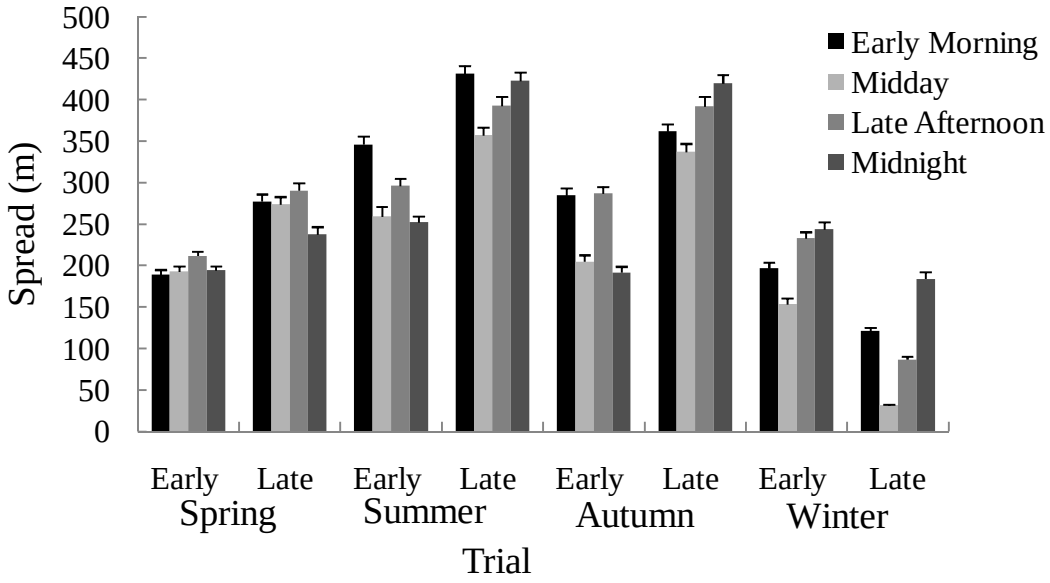


Figure 2.5. Mean and standard error of the spread per period of the day of a free-ranging cattle herd (N = 11) during eight trials of three weeks from Sept. 2007 to Aug. 2008.

Animal activity also affected herd spread. The spread of cattle herd during traveling was significantly smaller ($P < 0.01$) than when they were grazing or resting during late summer through early winter (Fig. 2.6). The average herd spread when traveling for these periods ranged from $X + SE$ = 135.28+24.24 m, N = 31 to $X + SE$ = 300.66+18.79 m, N = 213. The average herd spread during resting and grazing were similar in these periods and ranged from $X + SE$ = 201.35+4.24 m, N = 1,869 to $X + SE$ = 400.38+8.12 m, N = 996. Herd spread was significantly greater ($P < 0.01$) during grazing or resting in late summer and late autumn than in any other combinations of activity and season. Herd spread was smallest and most consistent for all three activities in late winter and early spring. Average herd spread, with all three activities combined, during these two periods was $X + SE$ = 160.46+6.06 m, N = 9,057.

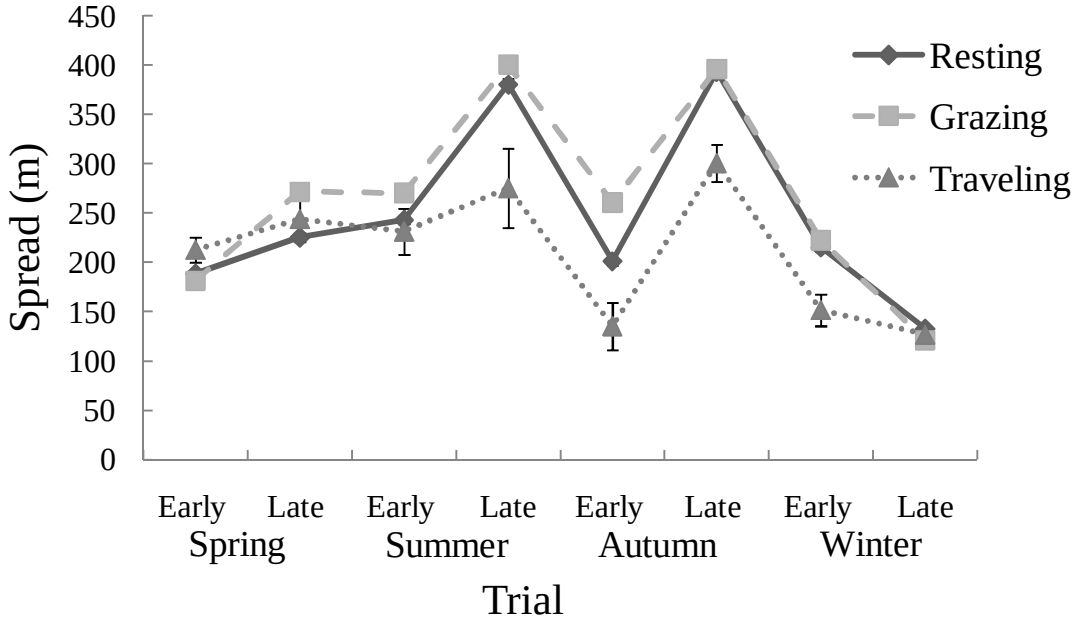


Figure 2.6. Mean and standard error of the spread per activity of a free-ranging cattle herd (N = 11) during eight trials of three weeks from Sept. 2007 to Aug. 2008.

Discussion

Foraging behavior of ungulates is influenced by processes that occur at different spatial and temporal scales (Bailey et al. 1996; Johnson et al. 2002). In turn, these scale-dependent processes interact to affect animal response to environmental fluctuations, yet few studies have considered these complexities. Our study of a free ranging cattle herd is one of the first to demonstrate the influence of multi-scale interactions between season, time of day and activity patterns on herd spread. Seasonal and diurnal scales are related to key processes that affect large herbivore distribution. Our study of cattle herd spread using GPS collars is also the first conducted in a brushy savanna environment. The relationship between cross-scale environmental variables and animal behavior is especially evident in this hot, semi-arid environment where sporadic and erratic precipitation leads to major fluctuations in forage quantity and quality (Sowell et al. 1999) and heat loading has a major effect an animal activity patterns.

To identify multi-scale relationships it is necessary to first dissect and understand the effects of each scale individually and then analyze how these scales and their effects relate to each other. Seasonal patterns of cattle herd distribution appear to be influenced by the interaction of seasonal fluctuations in forage characteristics and type of ecological region. At the broader seasonal temporal scale, the larger herd spread in our study occurred during the warm growing season and the smallest spread during the cold season when forage was less abundant. These results contrast with studies of grazing cattle conducted in northern, mountainous regions and other arid regions where cattle tend to forage and travel in larger and more compact groups during summer when forage is abundant and disperse to search for sparser resources in winter (Dudzinski et al. 1982; Lazo 1994; Howery et al. 1996; Harris et al. 2002, 2007). Northern rangelands and the Southern Plains have different climate regimes, where seasonal peaks in precipitation and temperature fluctuations influence forage growth patterns and, in turn, affect animal distribution and activity schedules. In semi-arid environments vegetative production is often limited by soil

moisture. In general, during dry winter periods cattle tend to congregate in riparian areas which maintain higher quality and availability of herbaceous standing crop during the dry non-growing season. The semi-arid climate in our study site was characterized by having most of its precipitation just prior to the hot summer season thus supporting maximum forage growth during summer. So in summer when larger amounts of green forage are available and animals are not as tied to standing water sources the cattle can disperse and be more selective in their diet, this resulted in larger herd spread and more homogeneous pasture utilization (Owens et al. 1991).

Diurnal patterns of cattle herd distribution appear to be influenced by the interaction of diurnal fluctuations in temperature and thermoregulatory actions. Throughout the year, herd spread was significantly lower during midday relative to the other three time periods (early morning, late afternoon, and midnight). Midday is the hottest part of the day and in South Texas even in winter midday temperatures can be stressful to the animals. The close associations of cattle during the hottest periods of the day are, in part, explained by thermoregulatory actions, where the cows rest in compact groups under shade trees to lose heat and regulate body temperature. Cattle might also be aggregating near water sources for osmoregulation and to prevent dehydration (Sato 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; DelCurto et al. 2000; Parsons et al. 2003; Harris et al. 2002, 2007; Cooper et al. 2008). A more in depth analysis of the influence of seasonality on daily spread shows that the greatest herd spread occurred at different times in the warm and cool seasons. During summer, herd spread was greatest in the early morning which is the coolest time of day. This pattern might be related to grazing periods which mostly occur during early morning and late afternoon hours and tend to generate a dispersive movement throughout the pasture (Stricklin et al. 1976; Sato 1982; Scoones 1995; Ganskopp 2001; Parsons et al. 2003). In winter, grazing activity was less influenced by high temperatures and greatest herd spread occurred around midnight, possibly as animals either moved to keep warm or dispersed away from the supplemental feeding sites. The differences in the diurnal variation of dispersion

of the herd between the warm and cool season demonstrate how a strong seasonal component influences the overall behavioral patterns.

Cattle management practices must be included as factors affecting herd spread because they can also influence the dispersion of animals across the landscape. The smaller spread of the cattle herd observed during in winter was likely influenced by the practice of providing supplemental feed and water to the cattle. This occurred year-round, but given the low forage production characteristic of the dry winter season, cattle appeared to be more responsive to the winter supplements and water possibly to meet energetic demands during that period of the year. Feeding the cattle a pelleted supplement aggregated the herd during the middle of the day. Similar patterns were found in winter in western rangelands where distribution of cattle was influenced more by supplemental placement of water and feed than buy the distribution of natural forage (Kie & Boroski 1996; DelCurto et al. 2005). These nutritional interactions between animal distribution and the environment have also been documented on other wild and domestic ungulates (e.g. goats, sheep, deer) in natural and managed settings (Parker et al. 2009), and in wildlife such as caribou in the woodlands of Canada where the patchy environment limits their distribution to small areas of available forage (Johnson et al. 2002).

Animal activities also lead to differences in the dispersion pattern of large herbivore herds and differences in the effect their presence has on the environment through grazing and trampling (Bailey 1995; Bailey et al. 1996). Grazing can alter plant community structure and intensive use of areas like trails and shaded resting may lead to soil compaction and disrupt plant growth. It is important to determine how activities vary spatially in order to better understand how they impact the landscape. In terms of herd spread per activity in semi-arid rangelands, herd spread was smaller during traveling than during resting and grazing, probably because the shrubs impede animal movement so the cattle follow established trails across the landscape as least effort pathways. Water runoff on such trails can lead to erosion on slopes but in flat terrain these trails may provide easy access for other animals, such

as deer, using the same habitat. In this study there was a dispersive movement of cattle during grazing probably due to the scattered nature of good forage plants in semi-arid environments. In more productive pasture settings the opposite pattern may be found, whereby cattle congregate to feed but disperse when moving to new areas (Shiyomi & Tsuiki 1999). In semi-arid areas the relatively sparse distribution of resources promotes the exploration of larger grazing areas or the division of the herd into subgroups thus increasing the group spread. Also, in shrub-dominated vegetation grazing herds may be dispersed by the shrubs that form visual barriers between animals and fragment the grass sward upon which they are grazing. In winter herd spread is smaller for all activities, visibility while grazing and traveling is improved as the shrubs shed their leaves, and individuals might be congregating around supplemental feeding and water areas. These findings further support our major conclusion that a coarse-scale process (i.e. seasonality) is controlling small-scale processes (i.e. diurnal and activity dispersion patterns) and shows the significance of studying these multi-scale relationships to more accurately detect the factors that influence animal distribution patterns that could be used for the development of predictive models of animal movement dynamics.

It is important to consider that this study was conducted using only one herd and one breed of cattle which limits the extent with which we can extrapolate our results on herd dispersive behavior to cattle in general or other group-living ungulates (Šárová et al. 2010). However, the characteristics of our herd and the conditions in the study area were typical of free-ranging cattle herds in semi-arid rangelands where the herd membership remained stable, animals were acclimated to their environment and there was minimal management of animals, as occurs in wild ungulate herds.

In synthesis, the seasonal pattern of herd spread was associated with forage availability and quality and the diurnal pattern was associated with temperature fluctuations affecting animal activity. Furthermore, herd spread at the diurnal scale seemed to be governed by the overall seasonal pattern because the spread at any time

of day varies seasonally due to forage availability and ambient temperature. The association between location and activity at the individual and herd level is key to determining landscape use intensity and provides valuable information for behavioral ecology studies. We were able to successfully discriminate between resting and traveling activities with an intermediate response of the grazing activity based on the distance between GPS fixes variable with a correct classification rate of 73%. These results partially contrast with Ungar et al. (2005) which suggest that the distance between GPS fixes is not a good predictor of activities. Also, cattle in this study spent a smaller proportion of time resting (28%) and a larger proportion of time traveling (24%) than compared to these authors who found 49% resting and 10% traveling observations in a study conducted in Oregon and Israel. Interactions between breed, terrain, climate, and vegetation characteristics might explain the difference in the proportion of time spent per activity between both studies (Kie & Boroski 1996; DelCurto et al. 2005). In this study, we used the Bonsmara breed, which is specially adapted for hot climates and it is able to graze further from water than less heat adapted cattle. Also, the topography in our site was relatively level and the vegetation was scattered. This could lead to longer travel times and higher dispersals than in more hilly terrain with a different forage dispersal patterns (Howery et al. 1996; Harris et al. 2002). Therefore, distances may be a good discriminator of activity in semi-arid rangelands with gentle topography, but may be inappropriate for different environments where different interactions of animal and environment occur.

3. GROUPING DYNAMICS AND DOMINANCE BEHAVIOR OF A CATTLE HERD IN A SEMI-ARID RANGELAND

Introduction

Herds of large herbivores have profound impacts on the environment, through their foraging behavior which affects plant community dynamics and ecosystem productivity and through mechanical disturbance of the soil due to trampling (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Harris et al. 2007). In turn, herds of large herbivores are influenced by spatial patterns of topography, forage and water distribution, environmental variables and social interactions with conspecifics (Bailey et al. 1996). However, we have limited understanding of the explicit spatio-temporal scales under which herds function.

Of particular relevance to ecological and social systems are cattle which are an important domesticated herding ungulate throughout much of the world (Van Soest 1994). They are the mainstay of many human cultures and provide a vital source of protein. To maximize the long-term productivity of cattle herds, previous studies have concluded that a better understanding of their herd spatial and temporal dynamics, dispersion regimes, grouping dynamics and dominance behavior is needed to optimize herd distributions on the landscape so as to maintain a sustainable and productive forage resource (Lazo 1994; Batterbury & Bebbington 1999; Harris et al. 2007).

Rangeland beef cattle herds, *Bos taurus* and *Bos indicus*, are a good model for empirical testing of large herbivore herd movement patterns and social interactions (Šárová et al. 2010). They combine the advantages of wild and domestic study animals because they have been maintained long enough for social dominance to be established within the herd and they can follow natural daily and seasonal rhythms with minimal human intervention, yet they offer ease of observation and handling (Reinhardt 1982; Šárová et al. 2010).

Free-ranging cattle herds are organized into sub-herds and individuals that form a fusion-fission social structure (Lazo 1994; Sowell et al. 1999; Harris et al. 2007). Sub-herds are often thought to be determined by strong social associations dependent on matriarchal families (Reinhardt & Reinhardt 1981; Harris et al. 2007). However, Howery et al. (1996) concluded that individuals in a sub-herd are not strongly associated and are a product of gregariousness rather than strong social groups. The exact nature of bonding may depend on the degree of management by humans, cattle are bought, sold, and moved to different areas dependent on rangeland conditions and economic forces (Kilgour 1972; Harris et al. 2007). Although the nature of these herd social associations is not fully understood, they could have direct influence on the evenness of pasture use, because strong cohesion between herd members might limit exploration of unused pastures by individual animals (Launchbaugh & Howery 2005) and cause overgrazing in other areas.

Many studies have identified topography, water location, shelter and forage characteristics as the main factors governing the distribution of cattle (Hinch et al. 1982; Owens et al. 1991; Bailey 1995; Ganskopp 2001; Harris et al. 2002; Bailey 2004, 2005). Few consider the social hierarchies that influence individual access to resources and thus influence spatial distribution within and between herds (Šárová et al. 2010). Social dominance occurs when the behavior of one animal is affected by the presence or threat of another animal (Bennet & Holmes 1987; Sowell et al. 1999; Šárová et al. 2010). Frequently dominant animals limit the access of subordinates to resources such as food. These social hierarchies may be indiscernible during times of ample resource availability but become evident during periods of low resource availability. In cattle, the most dominant animals have priority to feed, shelter and water and individuals are able to recognize the relative rank of other animals within the herd (Friend & Polan 1974; Arave & Albright 1981; Grant & Albright 2001). Social interactions are mostly passive, in which subordinates avoid conflict by monitoring their spatial relationship relative to dominant animals. However, there are instances where dominance ranks become evident through rapid head-to-head, neck

and side regions attacks (Wagnon et al. 1966; Grant & Albright 2001). Social dominance has been strongly associated with age, body weight or height, seniority and breed (Friend & Polan 1974; Arave & Albright 1981; Stricklin 1983; Grant & Albright 2001; Harris et al. 2007). Contrary to male social groups, female social groups exhibit a permanence of status among females and tend to be stable (Harris et al. 2007). Dominance among cows seems to be based on mutual familiarity, where individuals prefer to be in close proximity to herd members with similar rank (Syme et al. 1975; Arave & Albright 1981; Bennet & Holmes 1987). Dominance behavior affects the spatial associations among members of a herd where low ranked cows tend to position on the periphery of the group and dominant animals in the center of the herd according to the selfish-herd principle (Wagnon et al. 1966; Šárová et al. 2010). This behavior can have negative effects on subordinate individuals especially during periods of limited and patchy resources (e.g. droughts) when their access more productive areas is limited by their avoidance of the dominant animals. Such limitations negatively affect the weight gain of the animal and overall herd productivity.

Although previous studies have addressed some questions regarding the relationship between spatial interactions and social dominance in a cattle herd, they do not fully examine the explicit spatio-temporal parameters that characterize a herd or sub-herd throughout the year (Friend & Polan 1974; Arave & Albright 1981; Stricklin 1983; Grant & Albright 2001; Harris et al. 2007; Šárová et al. 2010). A major limiting factor for studying subgroup dynamics within herd systems is defining the spatial extent of subgroups (Harris et al. 2007). Specific knowledge of the broader spatial scales that defines the herd and the finer spatial scales that detect grouping dynamics year-round are necessary to understand the spatial perspective under which a cattle herd functions and perceives the landscape. With this kind of analysis it would be possible to determine the seasonal variations in subgroup formation and group dispersion throughout the pasture. However, more information is needed to better understand how dominance behavior affects group spatial

distribution in large herbivores, such a beef cattle, and how it varies seasonally particularly in a semi-arid rangeland where resources are often limited and erratic. The aim of this study was to increase our understanding of cattle herd spatial and temporal characteristics, seasonal grouping dynamics and its relationship to dominance ranks. Our specific objectives were to (1) determine the spatio-temporal parameters that characterize a cattle herd using GPS technology, (2) explore sub-herd dynamics using association techniques at different spatial thresholds and (3) determine the relationship between herd membership, spatial associations and dominance ranks.

Methods

Study site description

This study site is a 100-ha ranch in Uvalde, Texas (lat 29°19’8.584”N, long 99°42’54.161”W), located in the transition zone of two ecological regions, the Edwards Plateau and the South Texas Plains. Topography of this region is mostly level with gentle undulating planes (Taylor et al. 1999). Uvalde County has a semi-arid climate characterized by dry winters and hot, humid summers (USDA 1976). Average annual precipitation is 406 mm in west Uvalde with substantial inter-annual variations. Over 2/3 (68%) of the precipitation occurs during the warm season, May through October, usually with the highest amount of rainfall in May followed by a second rainfall peak in September. This area has a wide range in temperature with average temperatures ranging from 2.9°C in the winter to 36.7°C in the summer. The growing season lasts 340 to 360 days.

Soils in the ranch are mostly Montell clay (0 to 3% slope) characterized by gently sloping, deep, calcareous soils formed in clayey alluvium on outwash plains (Clay Flat range site; USDA 1976). The ranch was externally fenced and had no natural hydrological sources, but had two water tanks. A network of dirt roads covered the pasture to facilitate cattle and deer management. The ranch is part of a 457-ha property that was under a continuous/year long grazing schedule with

light/moderate stocking rate (15 ha/AU stocking density). This system provided no resting period for vegetation and the herd was hay-fed year-round.

The study area had a 29.4% woody cover composed by low-growing, thorny vegetation that formed dense mottes of small trees and shrubs with a grass matrix. Small trees of live oak, (*Quercus virginiana*), forms mottes scatted throughout the landscape, these are surrounded by a diverse variety of shrubs. The dominant shrubs inside the ranch are catclaw acacia (*Acacia greggii*), guajillo (*Acacia berlandieri*), Texas persimmon (*Diospyros texana*), agarita (*Mahonia trifoliate*), whitebrush (*Aloysia gratissima*), hogplum (*Colubrina texensis*), guayacan (*Guaiacum angustifolium*), honey mesquite (*Prosopis glandulosa*), twisted acacia (*Acacia schaffneri*), spiny hackberry (*Celtis ehrenbergiana*), and cenizo (*Leucophyllum frutescens*). Succulents like Texas pricklypear (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), and Yucca spp. are also common. Herbaceous species are mostly composed of Halls panicum, *Panicum hallii* var. *hallii,* hairy tridens (*Erioneuron pilosum*), common curlymesquite (*Hilaria belangeri*), Texas grama (*Bouteloua rigidiseta*), sideoats grama (*Bouteloua curtipendula* var. *curtipendula*), threeawn sp. (*Aristida* spp.), plains bristlegrass (*Setaria leucopila*), slim tridens (*Triden muticus* var. *muticus*), red grama (*Bouteloua trifida*), and Texas wintergrass (*Nassella leucotricha*). Common forbs include cardinal feather (*Acalypha radians*), Indian mallow (*Abutilon fruticosum*), orange zexmenia (*Wedelia texana*), frostweed (*Verbesina virginica*), ruellia (*Ruellia metzae*), ragweed (*Hymenopappus artemisiifolius* var. *artemisiifoliu,),* silverleaf nightshade (*Solanum elaeagnifolium*), hairy tubetongue (*Justicia pilosella*), cedar sedge (*Carex planostachys*), and prostrate lawnflower (*Calyptocarpus vialis*) (R. Cooper personal observation; TAMU Uvalde Herbarium, 2008).

Global positioning systems collars and animal selection

Currently, GPS, integrated with GIS provide the ability to capture the spatial interactions among members of a herd in much greater detail than field observations

or very high frequency (VHF) tracking (Ganskopp et al. 2000, Ungar et al. 2005). These advances in spatio-temporal data acquisition are used to track animal movement and landscape use to determine the biotic and abiotic factors that influence such movement patterns (Ungar et al. 2005). These technologies provide accurate location of individuals making it is possible to relate this spatial information to grouping dynamics and social interactions.

Collars containing GPS receivers (Lotek GPS 3300LR; Lotek Engineering, Newmarket, Ontario, Canada) were placed on 10 randomly selected individuals from a single herd of 31 free-ranging Bonsmara cows (*Bos taurus*). The animals were five to six years old and had an average weight of 1193.2±38.4 kg during the study period (Table 3.1). The herd has been in the study site since birth. The 10 selected individuals and their respective GPS collars were kept constant throughout the study. Animals were handled according to Texas A&M University System approved animal use protocols (AUP 2007-167). The selected individuals were isolated from the rest of the herd during the study period to avoid the influence non-collared cows on the behavior and distribution of the study group, which may bias the interpretation of spatial analyses between members of the group. Changes in the natural behavior of the selected individuals due to separation from the original herd were expected to be minimal because these were older animals accustom to regular management actions and this is more of a problem with younger individuals (Harris et al. 2007).

Table 3.1. Cow identification numbers, dominance rank, weight, age, udder, condition, frame, temperament, and muscling score of animals at the beginning of the study

Cow ID	Dominance rank	Weight (kg)	Age (yr)	Udder score[1]	Condition score[2]	Frame score[3]	Temp. score[4]	Muscling score[5]
2039	1	1286	6	1	5	6	1	4
2031	2	1306	6	2	6	7	1	4
2022	3	1140	6	2	5	7	1	3
2003	4	1162	6	1	5	7	1	3
3045	5	1306	5	1	6	7	2	3
2026	6	932	6	1	5	6	1	2
3050	7	1314	5	1	6	6	1	4
3002	8	1224	5	1	6	7	1	4
3560	9	1090	5	1	5	7	2	2
3028	10	1172	5	1	5	6	1	4
Average		1193.2	5.5	1.2	5.4	6.67	1.2	3.3

[1]Udder score: 1 = Balanced udder w/functional well placed teats, 2 = Unbalanced udder,
3 = Teats too large, 4 = Teats too small, 5 = Pendulous
[2]Condition score: 1-9 with 9 being fattest
[3]Frame score: Cattle skeletal size; Low frame scores are descriptive of cattle which are
short in stature for their age, tend to be early maturing, and finish for slaughter and mature at lighter body weights
[4]Temperament score: 1 = Docile, 2 = Restless, 3 = Nervous, 4 = Flighty, 5 = Aggressive,
6 = Very aggressive
[5]Muscling score: 1-5 with 5 being extremely well muscled and 1 being lightly muscled

The social dominance ranking was determined with a test supervised by experienced observers which consisted in recording antagonistic interactions (e.g. bluffing, head butting and fights) during feeding sessions in the feedlot. To facilitate observation of the interactions during the dominance test, the herd was divided into smaller subgroups (4-5 individuals). Ranks were assigned based on the individuals

that had higher priority to feed (Arave & Albright 1981; Stricklin 1983; Bennet & Holmes 1987; Harris et al. 2007). Ranks ranged from one to ten with one being the most dominant individual and ten the most subordinate.

Sampling period and data processing

The GPS collars provided information on location, date, time and ambient temperature every five minutes. Location was accurate to within 2m after differential correction (Lotek 2006). Spatial data with successive records separated by short time intervals (e.g. 5 min.) and the non-random movement of animals can produce distance serial autocorrelation (Swihart & Slade 1997; de Solla et al. 1999). Preliminary analyses (Perotto-Baldivieso et al. In press) indicate that 120 minutes intervals between GPS fixes can significantly reduce autocorrelation. In consequence, positional data was recorded at synchronized fix intervals every 120 min for all 10 individuals for 21 days per trial. Two sampling trials were conducted during the 2008 winter season (December 2008 and January 2009) and two trials during the 2009 summer season (June and August 2009) to compare effects of seasonality on the grouping behavior. Winter season represented the period of low resource availability which was compared to summer when forage resources were more abundant to determine the relationship between grouping dynamics and dominance ranking. Dominance behavior was expected to be more evident in winter when resources are limited (Sowell et al. 1999; Grant & Albright 2001).

At the end of each period data was retrieved from the collars and differentially corrected using N4 v.1.2138 Differential post-processing software (Lotek 2006; Base Station Del Rio, TX; NOAA 2007). When differential corrections were not possible, an uncorrected position was used (Ganskopp & Johnson 2007). When no collar integration was obtained, series of three consecutive records were interpolated to complete the data set. If more than three successive fixes was not obtained, that portion of the dataset was omitted from analyses (Ganskopp & Johnson 2007).

Grouping dynamics and statistical analysis

We used association matrices based on cow positional information obtained from GPS collars and the association software package, ASSOC1, (Weber et al. 2001), to analyze associations dynamics within the herd (Harris et al. 2007). This software uses association matrix, association pattern and pattern recognition to provide data on the spatio-temporal association of animals using a spatial and temporal threshold defined by the user. The spatial threshold is the maximum straight-line-distance at which any two individuals can be considered associated. Temporal threshold is the minimum percent of time two individuals have to spend together over the sampling period to be considered associated. To assign individuals into a group, the software selects a template grid using the individual(s) demonstrating association with the largest number of other individuals. Then, each individual association grid is compared to the template grid(s) to determine percent similarity. Individuals showing a similarity to the template grid exceeding the temporal threshold are grouped into the same subgroup. A more complete description of the software and its operation can be found in Weber et al. (2001) and Harris et al. (2007).

Small spatial thresholds and short increments allow the investigation of subtle subgroup formations and the spatial extents that are relevant to cattle herd dynamics. Coarser spatial thresholds identify at what distance the individuals start behaving as a single unit herd. The coarser spatial thresholds selected were 25m, 50m, 75m, 100m, 125m, 150m, 175m, 200m based on field observations of herd spatial extent, size of the study site and previous studies of animal associations (Harris et al. 2007). Once the delineations of the herd were determined, we conducted a more detailed analysis of herd membership using smaller spatial increments of 5m which is within the limitations of GPS error and is appropriate for the size of cattle.

To determine whether dominant or subordinate animals were closer to the center of the herd we used the center of gravity of the herd by calculating the average X and Y coordinates of the 10 individuals for each GPS fix on each trial. We then, obtained the Euclidean distance from each individual to the center of the herd. Spatial and temporal association calculations were summarized to estimate the mean and standard error for all trials. Mean comparisons were conducted to examine the overall seasonal patterns of spatial and temporal associations. Kruskal-Wallis (H) one-way analysis of variance on ranks Test ($\alpha = 0.05$) was used to examine statistical differences in the average temporal association of the herd between seasons and spatial thresholds and between the distance of individuals to the center of gravity. Herd membership, group size, number of groups and mean percent similarity were also summarized and compared between trials. To further investigate the relationship between spatial associations and dominance rank, we calculated the average rank of the herd at each spatial threshold increment for each trial to determine whether dominant or subordinate individuals had a higher spatial association. For example, if the average dominance rank decreases (higher ranking number) with an increase in the spatial threshold, then lower ranking animals are being added to the herd (were farther apart) hence higher ranked (dominant) animals had a higher spatial association.

Results

Spatio-temporal parameters that characterize a cattle herd

The variation in temporal association and changes in spatial threshold between trials of the same season was insignificant (Figs. 3.1 and 3.2). In other words, the animals did not spent more time closer to each other for all spatial thresholds during early summer (early summer; $X + SE = 70.95+0.94$ %, $N = 36$) and early winter (early winter; $X + SE = 77.19+0.85$ %, $N = 45$) than compared to their respective late summer (late summer; $X + SE = 56.84+0.99$ %, $N = 36$) and late winter trial (late winter; $X + SE = 71.85+1.39$ %, $N = 45$; Figs. 3.1a and 3.1b).

Therefore, summer trial and winter trial data can be combined. In terms of temporal associations between animal pairs in the herd, when the two trials for each season were combined, winter trials had significantly higher percent temporal association at all spatial thresholds ($X + SE$ = 74.52+0.81 %, N = 90) than compared to the summer trials ($X + SE$ = 63.90+1.08 %, N = 72; H_{15} = 985.97, $P < 0.05$; Fig. 3.1). During the winter season individual pairs spend, on average, a larger percent of time in closer proximity to one another than during the summer season. Although, the percent temporal association of animal pairs during all four trials tended to decrease as the spatial threshold decreased this relationship was not significant (Figs. 3.1 and 3.2).

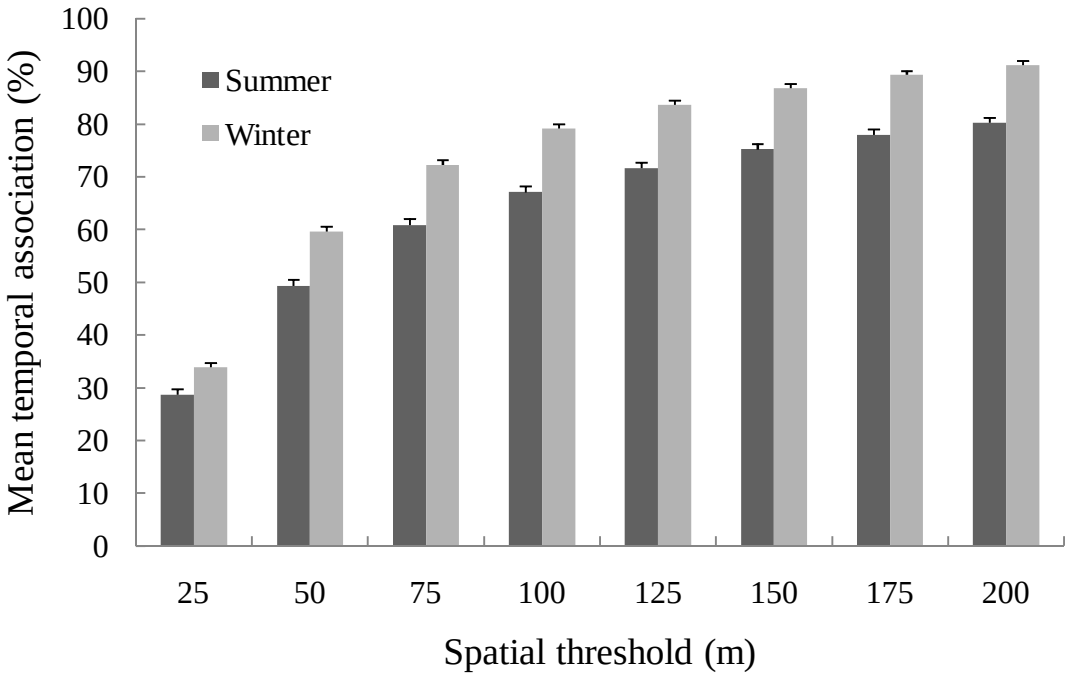


Figure 3.1. Mean and standard error of the temporal association (%) spent per cow pair within specified spatial thresholds (25 – 200m) of a free-ranging cattle herd (N = 10) during a summer and a winter trial each composed of six weeks from December 2008 to August in a Texas rangeland.

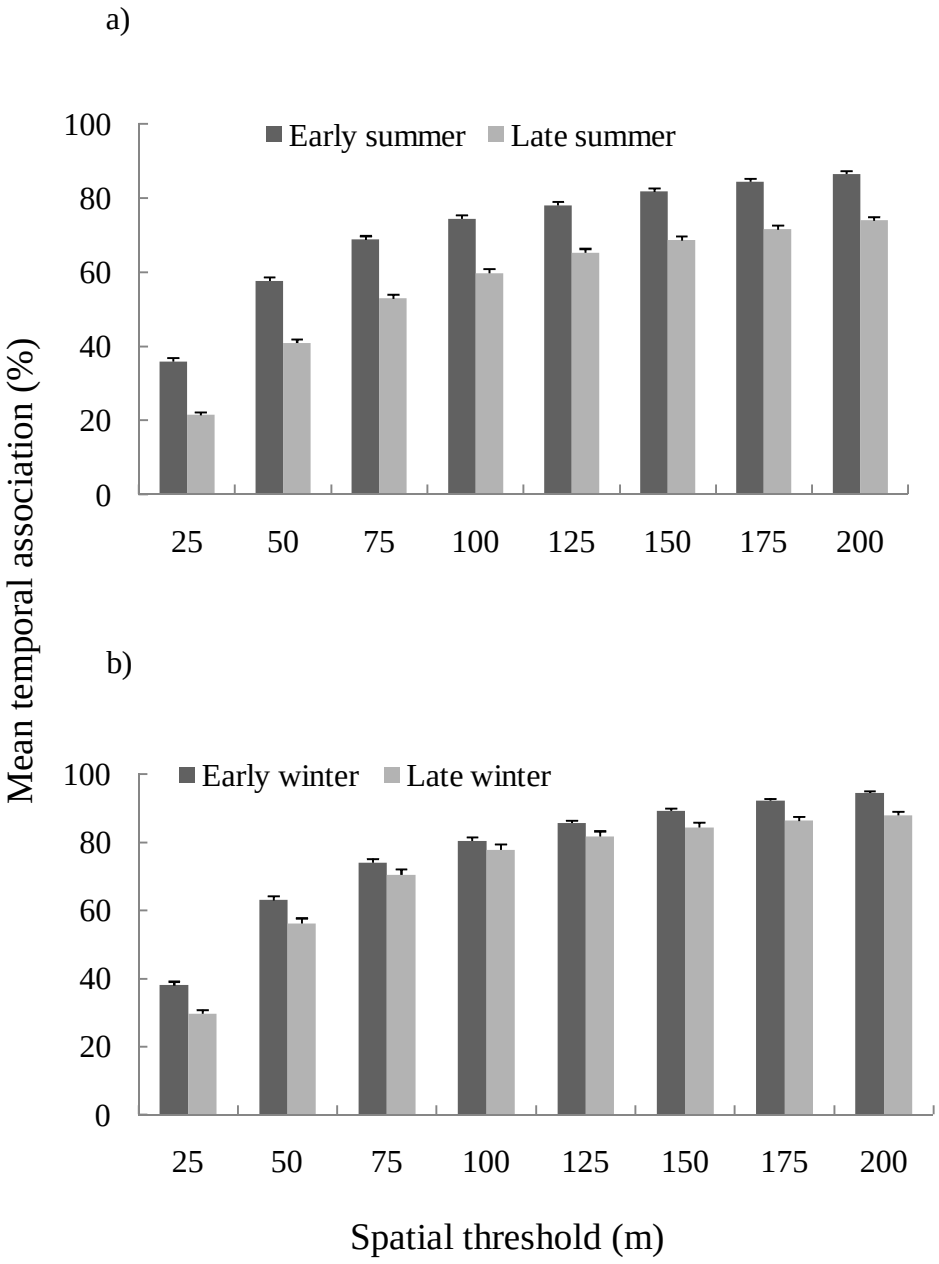


Figure 3.2. Mean and standard error of the temporal association (%) spent per cow pair within specified spatial thresholds (25 – 200m) of a cattle herd (N = 10) during (a) two summer trials and (b) two winter trials each composed of three weeks from December 2008 to August 2009 in a Texas rangeland.

The average percent temporal association when all spatial thresholds and trials were combined was 70%. In other words, cow pairs spent, on average, 70% of the time within 25 to 200m of each other. We used this temporal association value to define the herd parameters and to consider animals associated for our subsequent objectives.

Using a 70% temporal threshold, we were able to identify the spatial thresholds where individuals start behaving as a single unit herd for each trial. These were: early summer: 100m**,** late summer: 225m**,** early winter: 75m and late winter: 125m (Table 3.2). If we combine the two trials for each season into summer and winter we find that during the summer season all animals were found, on average, within 162.5m of each other, whereas during the winter season all animal were found, on average, within 100m of each other. Thus, during summer animal were farther apart than during winter. Also, during the early season trials, animals started behaving as one unit at shorter spatial thresholds, thus closer to each other, than compared to their respective late season trials. Conversely, we were also able to identify at what spatial threshold each member of the herd behaved as individuals alone for each trial. These distances were: early summer: 25m, late summer: 75m, early winter: 25m and late winter: 25m. All trials, except late summer, showed that no cow pairs spent 70% or more of the time within 25m of each other. For the late summer trials, cow associations started to appear at 100m.

Table 3.2. Association analysis of a cattle herd (N = 10) using different spatial thresholds for four trials each of three weeks. Number of individuals associated with group template, mean percentage, and standard deviation of similarity for individuals as compared to group templates. The temporal threshold was maintained at 70 percent

	Spatial threshold (m)							
Parameter	**200**	**175**	**150**	**125**	**100**	**75**	**50**	**25**
early summer								
Number Associated	9	9	9	9	9	8	3	0
Mean % Similarity	100	100	100	97.5	78.6	56.5	17.3	0
SD	0	0	0	4.7	19.5	29.9	33.7	0
late summer*								
Number Associated	8	8	8	4	4	0	0	0
Mean % Similarity	75.9	63.2	54.6	36.3	12.5	0	0	0
SD	25.6	32.7	34	32.8	33.6	0	0	0
early winter								
Number Associated	10	10	10	10	10	10	5	0
Mean % Similarity	100	100	100	100	96.1	76	36	0
SD	0	0	0	0	6.8	18.5	41.2	0
late winter								
Number Associated	10	10	10	10	9	8	2	0
Mean % Similarity	100	98	92.8	89.9	83	70.6	11.1	0
SD	0	4.1	12.7	19.5	23.8	39.3	32.3	0

*last individual found at 225 m

Mean % Similarity refers to how similar the pattern of association was between individuals and the template individual (a template individual is an individual demonstrating the largest number of associations in the herd).

Analysis of sub-herd formation using association techniques at different spatial thresholds

A more detailed analysis of grouping dynamics using 5m increments revealed that both summer trials showed subgroup division at intermediate values of their respective spatial threshold range (Table 3.3). During early summer, two groups (composed of two individuals and six individuals) were identified at 60-65m spatial thresholds and during late summer, two groups (composed of two/three individuals each) were identified at 100-115m spatial thresholds. The members in each sub-group remained consistent but no ranking, age or animal characteristic (e.g. frame score, temperament score) explained the membership pattern. Winter trials did not show subgroup division at any spatial threshold. The minimum spatial thresholds at which individuals started to show association and where the members of herd behaved as individual units was refined as: early summer: 50m, late summer: 100m, early winter: 40m, late winter: 50m. For all trials, except late summer, the majority of individuals became part of the herd unit at approximately 70m.

Table 3.3. Number and size of groups using spatial thresholds with 5m increments of a free-ranging cattle herd (N = 10) for four trials of three weeks. Smallest spatial threshold for each trial was selected when animals in the herd behaved as individual units and the largest spatial threshold when the herd behaved as one unit (all animals were included in the herd). The temporal threshold was maintained at 70 percent. Number of groups represents number of sub-herds

Parameter	**Spatial Threshold (m)**																				
early summer (25-100 m)	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100					
Number of individuals	0	0	0	0	0	3	4	8	8	7	8	8	8	8	8	9					
Number of groups	0	0	0	0	0	1	1	2	2	1	1	1	1	1	1	1					
Number of individuals per group	0	0	0	0	0	3	4	2/6	2/6	7	8	8	8	8	8	9					
late summer (75-150, 225 m)	75	80	85	90	95	100	105	110	115	120	125	130	135	140	145	150	225				
Number of individuals	0	0	0	0	0	4	6	6	6	4	4	7	7	7	8	8	9				
Number of groups	0	0	0	0	0	2	2	2	2	1	1	1	1	1	1	1	1				
Number of individuals per group	0	0	0	0	0	2/2	3/3	3/3	3/3	4	4	7	7	7	8	8	9				
early winter (25-75 m)	25	30	35	40	45	50	55	60	65	70	75										
Number of individuals	0	0	0	2	4	5	6	8	8	9	10										
Number of groups	0	0	0	1	1	1	1	1	1	1	1										
Number of individuals per group	0	0	0	2	4	5	6	8	8	9	10										
late winter (25-125 m)	25	30	35	40	45	50	55	60	65	70	75	80	85	90	95	100	105	110	115	120	125
Number of individuals	0	0	0	0	0	2	4	7	8	8	8	8	8	8	9	9	9	9	10	10	10
Number of groups	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
Number of individuals per group	0	0	0	0	0	2	4	7	8	8	8	8	8	8	9	9	9	9	10	10	10

Relationship between herd membership, spatial associations and dominance rank

There did not seem to be a clear, consistent and significant pattern of any particular ranking category to position closer to the center of the group than other members for any trial (Fig. 3.3). In other words, high ranking animals did not have a significantly different distance to the center of the herd than low ranking animals. Interestingly, during late winter the most dominant individual was significantly farthest from the center of the herd than compared to most other individuals ($X + SE$ = 145.45+11.91m, $N = 250$; $H_9 = 48.15$, $P < 0.05$; Fig. 3.3d). Moreover, the overall distance from all members to the center of the herd varied between all seasons except between early summer and late winter ($H_3 = 820.93$, $P < 0.05$). early summer had an average distance to the center of the herd of $X + SE$ = 78.15+7.32 m, $N = 155$, late summer $X + SE$ = 155.77+10.36 m, $N = 278$, early winter $X + SE$ = 54.98+4.14 m, N = 250 and late winter $X + SE$ = 81.80+6.47 m, $N = 250$. Thus, individuals were the farthest (more dispersed) from the center of the herd during late summer and closest (more aggregated) during early winter.

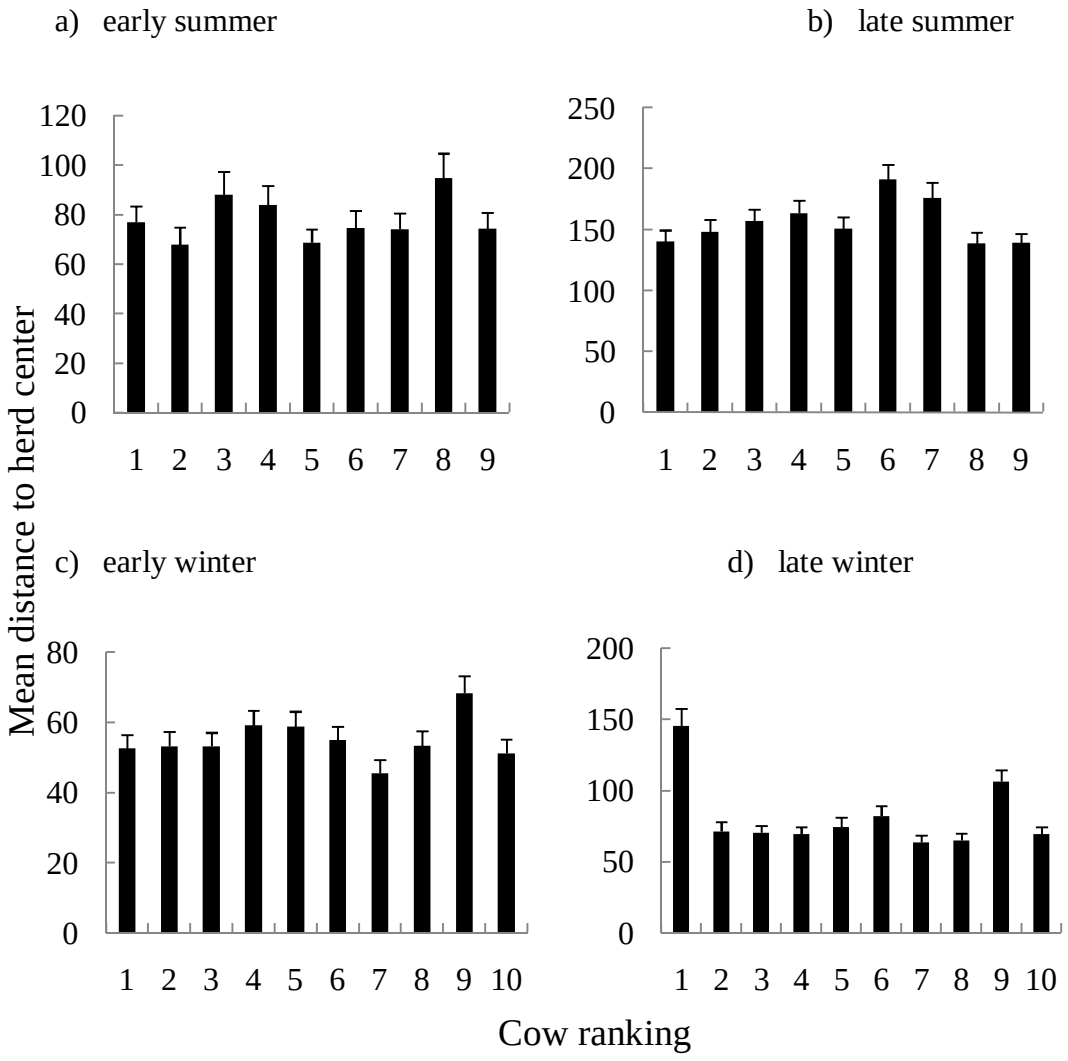


Figure 3.3. Mean and standard error of the distance of each individual to the center of herd, classified by dominance ranking, of a cattle herd (N = 10) during two summer and two winter trials each composed of three weeks from December 2008 to August 2009 in a Texas rangeland.

We also determined the average dominance rank of the herd at each spatial threshold (Fig. 3.4). If average dominance rank decreases with an increase in the spatial threshold then lower ranking animals are being added to the herd and dominant animals

had a closer spatial association than subordinate animals. At the smallest spatial threshold, early summer and early winter had an average herd dominance rank of $X + SE$ = 4.67+1.76, N = 3 and $X + SE$ = 4.00+3.00, N = 2 and at their largest spatial threshold they had an average herd dominance rank of $X + SE$ = 5.44+1.07, N = 9 and $X + SE$ = 5.5+0.96, N = 10 respectively, which is a slight increase in the average dominance rank of the herd. This means that lower ranking animals were being added to the herd as the spatial threshold increased, and higher ranking animals, which had a higher spatial association than subordinate animals, were part of the herd at smaller spatial thresholds. late summer had an irregular pattern of dominance ranking dynamics, but the overall pattern was an increase in the average dominance rank of the herd from $X + SE$ = 3.50+0.65, N = 4 at its smallest spatial threshold to $X + SE$ = 4.11+0.98, N = 9 at its largest spatial threshold. Thus, cattle were behaving similar to the early summer and early winter trials where dominant animals were, on average, closer to each other. late winter presented the opposite pattern where the average dominance rank of the herd greatly decreased from $X + SE$ = 9.00+1.00, N = 2 to $X + SE$ = 5.5+0.96, N = 10 as the spatial threshold increased. Hence, subordinate animals formed part of the herd at shorter distances between each other and so were closer to each other than the dominant individuals.

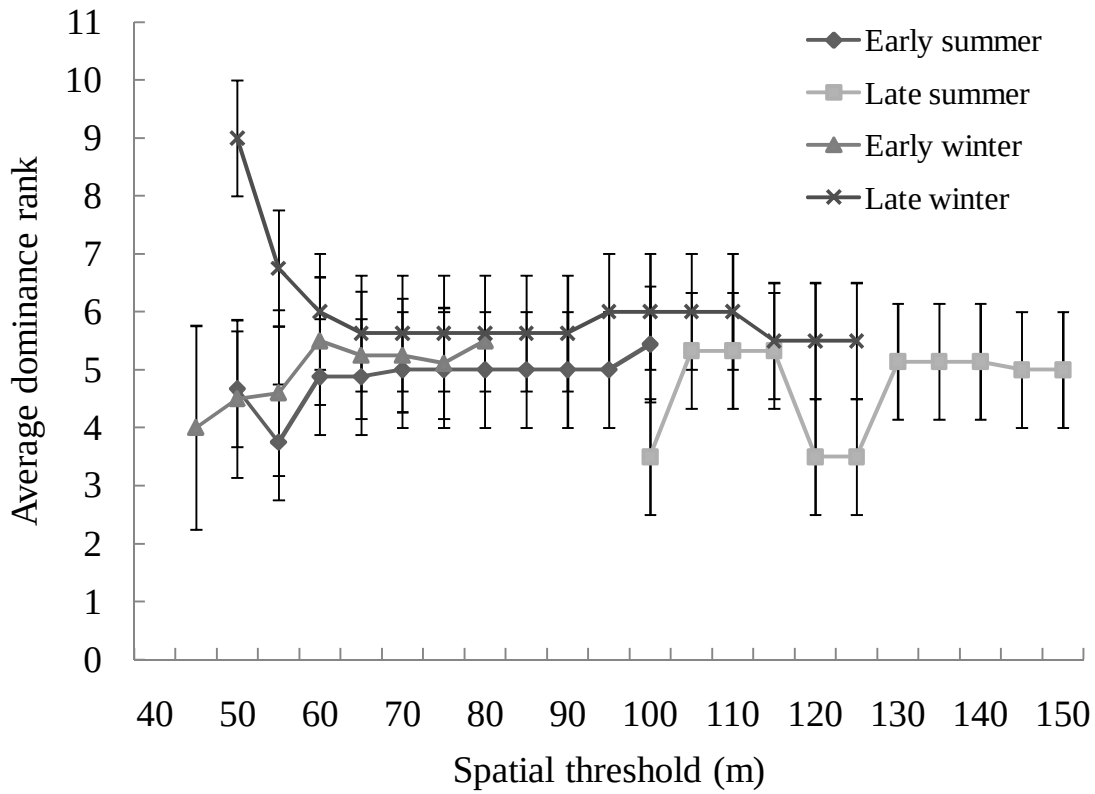


Figure 3.4. Mean dominance rank of the members included in a cattle herd (N = 10) at different spatial thresholds during four trials of three weeks in a Texas rangeland.

Discussion

Herd spread and social associations among members of a herd are important as they influence how members impact their environment. Also, when we compare our results with similar studies conducted in other areas it appears that the distribution of conspecific herd animals respond differently to environmental factors depending on the type of ecological region. In this shrub-dominated savanna, on a temporal basis, during the non-growing winter season, members of the herd spent more time closer to each other, thus behaving in a more aggregated spatial pattern than during the summer growing season when members dispersed. This stronger group aggregation during winter may be driven by seasonal changes in forage availability which reduces exploration of unused pastures and limit the evenness of landscape use (Launchbaugh & Howery

2005). The condition of the vegetation is one of the most important influences in the dispersive movement for grazing animals in savannas pastures (Sato 1982; Harris et al. 2002). In northern and mountainous regions cattle tend to travel in larger and more compact groups when forage is abundant (Dudzinski et al. 1982; Lazo 1994; Howery et al. 1996; Harris et al. 2002, 2007). However, in semi-arid environments, forage production is often moisture limited. Cattle congregate in areas with higher availability and quality of herbaceous standing crop that lasts into the dry non-growing season (Owens et al. 1991; Scoones 1995; Sowell et al. 1999). Moreover, in semi-arid areas of Texas, Owens et al. (1991) concluded that when large amounts of standing crop are accessible to cattle, they would be more selective and this resulted in greater herd spread and larger variations of pasture utilization. The congregation of animals in preferred areas can result in negative environmental and socio-economical impacts such as vegetation degradation, watershed contamination, soil compaction and erosion and unsustainable livestock ranching (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Harris et al. 2007). Characteristic of most savanna biomes, the semi-arid climate in our study site had highly seasonal rainfall patterns and most forage growth occurred in the hot summer months which might explain the larger dispersion of herd members at this time. This differential behavior in large herbivore aggregation patterns between northern and southwestern regions stresses the importance of studying organisms under many settings of topography and climate regimes to capture the full behavioral spectrum of animals.

The management regime of livestock appears to also influence the distribution of animals in the landscape. The aggregation of members of the herd during the dry non-growing winter season, might also be related to availability of supplemental feed and water. Although the management regime was kept constant throughout the year, cattle appeared to be more responsive to food and water supplementation during winter. Other studies have also found that, in western rangelands, the distribution of cattle during the non-growing season is mostly influenced by supplemental placement of water and feed (Kie & Boroski 1996; DelCurto et al. 2005). These nutritional interactions between

animals and its environment has also been documented on other ungulates (e.g. goats, sheep, deer) in natural and managed settings where they use physiological and behavioral mechanisms to cope with this seasonal variation in the nutritional value of the forage or browsing site (Sato 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; Harris et al. 2002; Parsons et al. 2003; DelCurto et al. 2005; Harris et al. 2007; Cooper et al. 2008; Parker et al. 2009). Hence, the degree of dispersion of the herd observed in our study could be explained by forage conditions associated with year-round changes of environmental variables and supplemental feed and water availability. This finding presents evidence of an interrelationship between seasonal fluctuations in forage availability and management regime that affects the distribution patterns of animals.

To better understand herd behavior we need to have a clear and consistent definition of herd spatio-temporal characteristics. Especially when the aim is to detect subtle changes in group dynamics such as sub-herd formation, herd size, dominance makeup and group spread. On a spatial basis, the information obtained through GPS technology and ASSOC1 association software allowed us to determine the basic temporal and spatial parameters that characterized our study herd. On a temporal basis, cow pairs spent, on average, 70% of the time within 25 to 200m of each other. This result is comparable to the field observations of Harris et al. (2007) who determined that cow pairs were within a similar distance threshold 67% of the time. Based on these results, animals that spend approximately 70% or more of the time in close proximity to another animal should be included as members of the group and this should capture most major group interactions. On a spatial basis, we were able to identify the spatial threshold where all individuals start behaving as single herd for each season based on a 70% temporal threshold. During the summer season all animals were found, on average, within 162.5m of each other whereas during the winter season all animal were found at a shorter distance of within 100m of each other. This finding further supports the idea that individuals in the herd behave in a more aggregated fashion during the non-growing winter season. The minimum distance at which individuals started to be included as members of the herd ranged between distances of 40-50m of each other for all trials

except during late summer where individuals started to be included in the herd at a distance of 100m. This type of spatio-temporal analysis allowed us to explicitly identify and detect the characteristics that define the herd. This is an important and essential step towards more accurate ethological studies of herd dynamics because it helps to focus analysis efforts at the spatial and temporal scales that are relevant to the animal's perspective and not necessarily to the investigator.

Furthermore, using GPS collar data accurate to 5m we were able to refine the spatial analysis to allow us to identify whether and at what distance the herd formed sub-herds for each season. Both summer trials showed the herd divided into two subgroups each whereas none of the winter trials showed subgroup division at any spatial threshold. Harris et al. (2007) in the Sierra Nevada foothills, also found that cattle herds split into subgroups of 2-6 members but, in contrast to our finding in Texas, he found that these subgroups formed when forage was least abundant. The dispersal of cattle during the growing season as seen in Texas might be favorable for the vegetation community, because this will be associated with a more distributed pasture use and less overuse of critical areas such as riparian areas. This finer analysis using smaller spatial threshold increments allowed us to detect subtle subgroup formations (e.g. during summer trials) and fine-tune to the spatial extents that are relevant to large herbivore herd dynamics and analysis in semi-arid rangelands. This finding shows the importance of studying movement patterns and grouping dynamics of herd animals at different spatial and temporal scales to better determine the various levels that affect animal behavior. One scale alone will not be sufficient to accurately understand the underlying mechanisms and responses of animals to the environment.

Social dominance appears not to play a major role in herd spatial associations of domesticated animals. Wild herd animals have evolved to form large groups for protection from predation and the group center is often occupied by the dominant (most of the time older) animals or by females with young so as to decrease the chance of being a victim of predation. Herding may also limit exposure to parasitic fly attacks by minimizing the distance between an individual and its neighbors (Stricklin 1983; Šárová

et al. 2010). Although we found evidence of dominant animals to be more closely associated in three of the four trials, these trends were relatively small. Also, our results showed that there was no consistent and significant pattern of any particular ranking category to position closer to the center of the group than other members. These results agree with Šárová et al. (2010) who found that dominant beef cattle were not positioned more centrally than subordinate animals, however, these authors did find that dominant animals were found closer to the front of the herd during traveling and grazing activities. Behavioral patterns observed in many wild herds might not be as evident in domestic livestock where artificial selection through genetics and management might have developed more tolerant (Grant & Albright 2001), less aggressive and less dominant animals. Moreover, our study site did not have any large predators that might have provoked such type of protective behavior. The only exception occurred during late winter where the most dominant individual was significantly farther from the center of the herd. This could be attributed to the cow tending the nursery of calves that were present during that study period. Prior studies have not come to any consistent conclusion on the relationship between dominance and spatial associations among members of cattle herds, (Arave & Albright 1981; Hinch et al. 1982; Harris et al. 2007). Even though the herd in our study seemed to exhibit slight increases or decreases in the average dominance rank of the herd as we increased the spatial threshold, these changes appeared to be small (except for late winter) suggesting that dominance rank does not play a major role in the distance between individuals that form the herd. Perhaps, the social influence on the spacing pattern within the herd might be stronger on larger herds (e.g. 200 individuals) or in areas with very limited resources where the benefits of dominance will be magnified and behavioral responses more evident. On the other hand, during late winter highly subordinate individuals were, on average, 10m closer to each other. Thus, lower ranking animals seem to tend to stay closer together during the non-growing season. The relationship between dominance, competition for feed, and spatial associations is more evident in situations with limited feeding space, which makes feed a defensible resource (Grant & Albright 2001). This kind of interactions might be

occurring in our study herd during this limiting period where subordinate individuals are staying closer together and maintaining a larger distance away from more dominant individuals. Lastly, the overall distance from all members to the center of the herd was smaller during the winter season and larger during the summer season, thus creating a more compact herd during winter. This aggregation pattern might be related to a combination of thermoregulatory actions and forage and supplemental feed availability. This suggests that there is a strong seasonal component and not so much a dominance effect is influencing herd dynamics in this brushy savanna.

It is important to note that this study was conducted using only one herd and one breed. This constrains the extent with which we can extrapolate our results on herd spatio-temporal distribution patterns, grouping dynamics and social associations to cattle in general or other group-living herbivores. Nonetheless, the characteristics of our herd and the conditions in the study area were typical of free-ranging cattle herds in semi-arid rangelands where the members were kept constant, minimal cattle and range management was performed and animals were accustomed to the site for many years before the study took place. For these reasons we did not expect our results to be unusual.

4. SEASONAL AND DIURNAL INFLUENCE OF RESOURCES AND SHADE PATCHES ON THE SPATIAL DISTRIBUTION OF A FREE-RANGING CATTLE HERD IN A SEMI-ARID RANGELAND

Introduction

Given the current critical status of habitat degradation and loss, species invasions and global climate change, there has been a great interest in more accurate and explicit studies of the factors that affect distribution of species (Ritchie et al. 2009; Butt 2010). Ungulates play essential roles both in natural environments where they shape the vegetation composition and structure and influence ecosystem function and in managed settings where they provide resources to human populations (Butt 2010; Goheen et al. 2010). Developing better predictive models of ungulate movement patterns is an important endeavor for assessments of the relationship between species distribution, ecosystem change and pastoralist livestock operations (Butt 2010). The behavior of ungulates is influenced by landscape structures and resources and the interaction of ecological processes that occur at different spatial and temporal scales (Senft et al. 1987; Bailey et al. 1996; Johnson et al. 2002; Seagle & McNaughton 1992; Weladji et al. 2002; Peters et al. 2004, 2006). As a consequence, flexible and opportunistic nutritional and physiological strategies develop from this spatio-temporal variability producing distinct spatial distribution patterns in both wildlife and livestock and in natural and managed settings (Scoones 1995; Seagle & McNaughton 1992; Parker et al. 2009). Moreover, due to physiological and nutritional needs, animals will tend to congregate in areas where the required resources or structures are available (e.g. forage, water, minerals, shade) which, in most cases, is not evenly distributed throughout the area (Belovsky 1984; Senft et al. 1987; Frixell 1991; Ganskopp 2001; Wallace et al. 1995; Cooper et al. 2006). For example, in dry environments where sporadic and erratic precipitation leads to fluctuations in forage production. Also, the forage is not equally distributed across the landscape, ungulates often exhibit uneven grazing distribution patterns as animals select areas of highly palatable forage in close proximity to water or

supplemental feeding sites (Frixell 1991; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Butt 2010). This selective foraging behavior, sometimes called matching, has been observed in many herbivores such as mule deer (*Odocoileus hemionus*), wapiti (*Cervus canadensis*), feral horses (*Equus caballus*), eastern grey kangaroos (*Macropus giganteus*), North American bison (*Bison bison*), caribou (*Rangifer tarandus*) and free-ranging domestic livestock (Senft et al. 1987; Bailey et al. 1996; Johnson et al. 2002). Another environmental variable that influences the movement pattern of wild and domestic ungulates, particularly in semi-arid, arid and desert environments of Africa, Middle East and North America, is diurnal temperature fluctuations which drive animals to seek shade to escape the heat for thermoregulation (Dudzinski et al. 1982; Bennet et al. 1985; Coppock et al. 1986; Lazo 1994; Howery et al. 1996; DelCurto et al. 2000; Cain III et al. 2006; Cooper et al. 2008). Other factors widely known to affect large herbivore movement are slope, plant species composition and morphology, strategic salt placement, brush control, burning or mowing, and wind patterns (Hinch et al. 1982; Senft et al. 1987; Owens et al. 1991; Bailey 1995; Ganskopp 2001; Harris et al. 2002; Bailey 2004, 2005).

Although previous studies have recognized these resources and structures as major influences on ungulate distribution patterns, most of them have been studied in isolation or using only one temporal scale that may not even be relevant to the animal's response to space or time (Senft et al. 1987; Johnson et al. 2002). However, to better understand ungulate movement patterns that coincide with their response to the environment it is essential to study their explicit spatio-temporal behavior across multiple scales to try to discern how scale-dependent biotic and abiotic factors interact and influence animal landscape use (Senft et al. 1987; Bailey et al. 1996; Johnson et al. 2002; Butt 2010). For example, more information is needed about ungulate use of landscape structures such as shade patches and resources such as water and supplemental feeding areas in response to seasonal changes in available forage biomass and seasonal and diurnal fluctuations in temperature in a level brushy savanna.

Ungulate distribution studies were usually based on field observations of a few animals and analyses of movement patterns were difficult to measure (Stricklin 1983; Turner et al. 2000, 2001; Harris et al. 2007). These studies have limited accuracy, few to no replications, and almost no night observations. Global positioning systems, integrated with GIS and remote sensing technologies, have been used to understand the relationship between landscape characteristics and animal movement dynamics (Ganskopp et al. 2000; Turner et al. 2000, 2001; Ungar et al. 2005; Butt 2010). These advances in geospatial data acquisition allows for the precise tracking of animal distribution and landscape use which can provide a new body of information useful for more accurate ethological studies and response to landscape structure and changes in the environment (Ungar et al. 2005). Many studies have already used these technologies to better understand ungulate movement patterns in mountainous and level rangelands of North America, arid and semi-arid environments in the Middle East and Europe and African savannas (Dudzinski et al. 1982; Bennet et al. 1985; Lazo 1994; Bailey et al. 1996; Coppock et al. 1986; Howery et al. 1996; DelCurto et al. 2000; Ungar et al. 2005; Harris et al. 2007; Cooper et al. 2008; Butt 2010).

Influence of available forage biomass

The optimal foraging theory relates the effects of food quality in influencing the diet composition and foraging strategies of animals (Seagle & McNaughton 1992). Herbivores must meet energetic demands by foraging selectively and efficiently and at the same time balance nutritional requirements. Ungulates as diverse as sheep and kudus can follows temporal changes in forage quality and availability and remember the relationships between food and their nutritional effect (Senft et al. 1987; Bailey et al. 1996; Wallace et al. 1995). The foraging decisions of animals at larger spatial and temporal scales can influence choices at lower levels. For example seasonal food availability has been shown to dominate diurnal cattle herd spread patterns (Chapter 2). Moreover, changes in cattle aggregation patterns during different seasons have been associated to seasonal changes in available forage biomass (Dudzinski et al. 1982; Sato

1982; Lazo 1994; Howery et al. 1996; Harris et al. 2002, 2007; Butt 2010). In arid environments, during the dry season when forage availability is low cattle congregate in areas, such as riparian zones, which maintain higher available herbaceous standing crop per unit area and higher quality forage than dry land rangeland (Owens et al. 1991). A pattern seen in semi-arid areas (Belovsky 1984; Owens et al. 1991) is that when large amounts of standing crop are accessible to ungulates they can be more selective in dietary choice. Searching for better quality forage results in greater herd spread and larger variations of pasture utilization. Given that forage biomass is one of the major factors that influence large herbivore movement, it is important to quantify the relative seasonal changes in vegetation biomass when investigating the causes of animal distribution patterns (Senft et al. 1987; Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Butt 2010).

When long-term field measurements of biomass availability are not available, remotely sensed estimates can serve as viable alternative (Butt 2010). Vegetation indices derived from various satellite platforms and sensors are dimensionless, radiometric measures that indicate the relative abundance and biological activity of green vegetation (e.g. leaf area index, percent green cover, green biomass) that function as surrogates for important biophysical vegetation parameters (Jensen 2005). Remotely sensed images can be used to estimate green biomass using the differential brightness between the red and near-infrared bands. Of the many different indices, the Normalized Difference Vegetation Index (NDVI) has been regarded as "the most robust indicator of available forage biomass" used in many ecosystems to determine the spatio-temporal variability of vegetation resources (Butt 2010). Although not a direct measure of biomass, NDVI is highly correlated with precipitation and primary productivity. Furthermore, it has been used for more than 30 years throughout the sub-Saharan Africa and has been described as the most reliable vegetation index of dried biomass characteristic of savanna ecosystems (Martiny et al. 2005, 2006; Butt 2010).

Vegetation shows differential brightness in the red and near-infrared parts of the electromagnetic spectrum (Gates 1970). Red light is strongly absorbed by photosynthetic

pigments in green leaves, whereas near-infrared is reflected by live leaf tissues. This means that areas with much green vegetation will appear very bright in the near-infrared and very dark in the red part of the spectrum. It is the process of glucose-making via photosynthesis that determines how a leaf appears on remotely sensed images (Jensen 2005). NDVI is calculated as:

$$\text{NDVI} = \frac{\partial NIR - \partial Red}{\partial NIR + \partial Red} \quad (1)$$

Where NIR is the reflectance from the near infra-red band and Red is the reflectance from the red band (Jensen 2005). This index ranges from -1.0 to 1.0 with vegetated areas with values greater than zero and negative values indicating non-vegetated surface features.

Remotely sensed environmental data coupled with GPS locations of animal distribution patterns has already proved useful for uncovering the grazing dynamics of both wild ungulates and domestic livestock in various environments (Bailey et al. 1996; Ganskopp 2001; Ungar et al. 2005; Butt 2010). Measurements of NDVI should prove beneficial to assess how seasonal changes in available forage biomass relate to patterns of ungulate use of landscape structures and resources in a brushy savanna.

Influence of shade patches

On a diurnal scale, in tropical and semi-arid environments during hot periods of the day animals shelter in shade to lose heat and regulate body temperature (Hirst 1975; Dudzinski et al. 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; Howery et al. 1996; DelCurto et al. 2000; Cain III et al. 2006; Cooper et al. 2008). Ungulates such as impala (*Aepyceros melampus*), wildebeest (*Connochaetes* spp.), zebra (*Equus* spp.), and waterbuck (*Kobus ellipsiprymnus*)have been observed to loaf in the shade during midday in South African woodlands and savannas ecosystems (Hirst 1975). Bennet et al. (1985) found that as air temperature increased cattle spent significantly more time under shade and reduced grazing time during the summer in a pasture in the dry tropics of

Rockhampton, Queensland. Even in more mountainous areas, Harris et al. (2002, 2007) reported that during the summer, the cows spent a larger amount of time under shade trees near water than during winter where they spent most of the time at warmer exposures and avoided shade trees. Even though these studies provide valuable information on cattle movement patterns they do not provide an analysis that includes both seasonal and diurnal information of animal positional data in a level terrain semi-arid rangeland.

Influence of water and supplemental feeding areas

Free-ranging herbivores must forage in an efficient way to meet energetic demands and balance nutritional requirements (Seagle & McNaughton 1992). Besides forage characteristics, proximity to water and supplemental feeding areas (in the case of managed animals) are factors frequently mentioned as proximal causes for ungulate foraging behavior, although the degree of the effect seems to be a function of the climate and landscape structure of the study site (Kie & Boroski 1996; DelCurto et al. 2005; Wallace et al. 1995; Cooper et al. 2006). On a seasonal basis, ungulates seem to congregate into small discrete patches where the required resources are most abundant and of higher quality (Johnson et al. 2002; Cooper et al. 2006). For example, during the non-growing season, Kie & Boroski (1996) and DelCurto et al. (2005) found that in the western rangelands of North America, distribution of cattle is mostly influenced by supplemental placement of water and feed. On a diurnal basis, ungulates have the tendency to aggregate during hot periods of the day to sites where water is readily available. This behavioral response has been documented in arid and semi-arid regions of tropical Africa (Coppock et al. 1986), rangelands of Australia (Dudzinski et al. 1982; Howery et al. 1996), southwest Spain (Lazo 1994), Tohoku, Japan (Sato 1982), rangelands of western United States (DelCurto et al. 2000; Parsons et al. 2003; Harris et al. 2007), and South Texas (Cooper et al. 2008). Thus, the spatial response of cattle to these resources seems to be a function of the interaction of process occurring at different temporal scales (e.g. seasonal and diurnal). The smaller spread of the cattle herd

observed in our previous study during the dry non-growing season could have been greatly influenced by a management regime (Chapter 2). The placement of supplemental feed and water occurred year-round, but given the low forage production characteristic of the dry winter season, cattle may have been more responsive to the winter supplements and water possibly to meet energetic demands during that period of the year. A more detailed analysis of the explicit spatio-temporal use of these resources by cattle should provide the necessary information to determine the relationship between cattle spread and water and supplemental feed placement.

We used a free-ranging cattle herd to better understand how landscape characteristics affect the spatial distribution group-living ungulates in a brushy savanna. The use of established herds of free-ranging cattle provides advantages of working with semi-wild animals in the sense that it allows for convenient handling of animals during the study period while permitting the animals to behave freely without restrictions and with minimal human interference (Reinhardt 1982; Šárová et al. 2010). Our objectives are to (1) use seasonal Normalized Difference Vegetation Index (NDVI) as an indicator of available forage biomass to explore its relationship to cattle herd movement dynamics, (2) determine the degree of seasonal use of shade patches by cattle at different periods of the day and (3) determine the seasonal and diurnal influence of water and supplemental feeding points on cattle distribution patterns.

Methods

Study site description

This study site was a 457-ha ranch in Uvalde, Texas (lat 29°19’8.584”N, long 99°42’54.161”W), located in the transition zone of two ecological regions, the Edwards Plateau and the South Texas Plains (Fig. 4.1). Topography of this region is mostly level with gentle undulating planes (Taylor et al. 1999). Uvalde County has a semi-arid climate characterized by dry winters and hot, humid summers (USDA 1976). Average annual precipitation is 406 mm in west Uvalde with substantial inter-annual variations. Over 2/3 (68%) of the precipitation occurs during the warm season, May through

October, usually with the highest amount of rainfall in May followed by a second rainfall peak in September. The average temperature ranges from 2.9°C in the winter to 36.7°C in the summer. The growing season lasts 340 to 360 days.

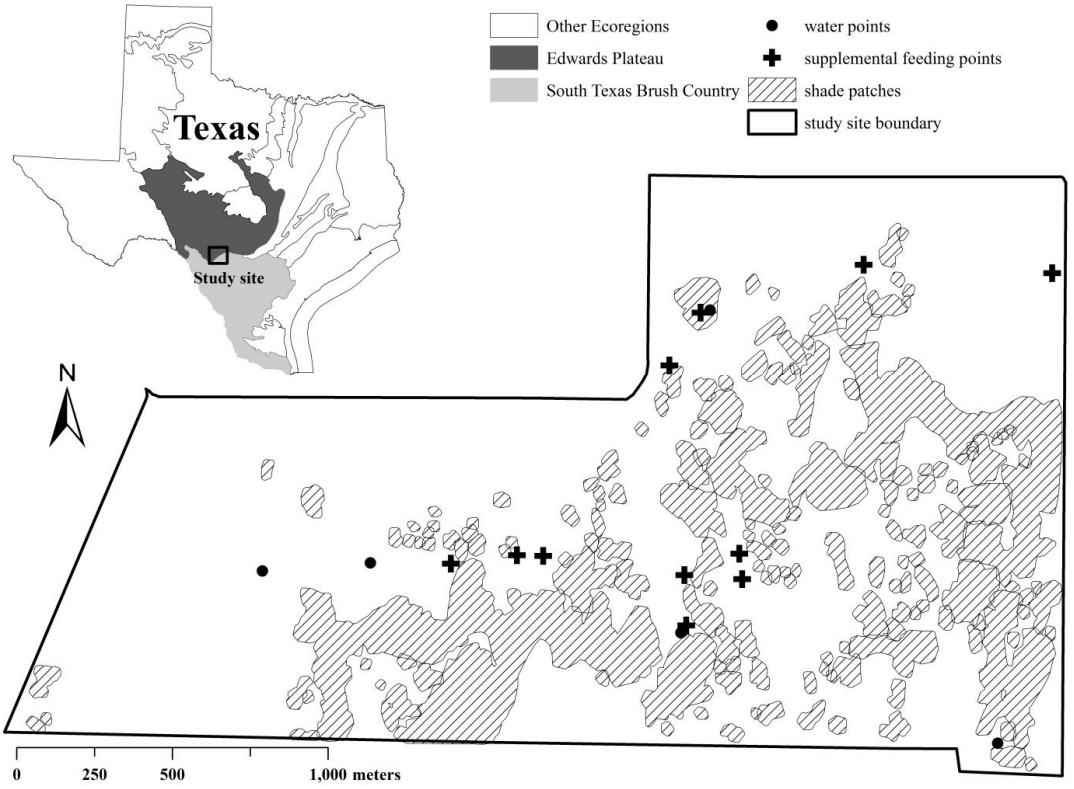


Figure 4.1. The 457ha study site is a gentle terrain semi-arid rangeland located between two ecological regions: Edwards Plateau and South Texas Brush Country, Texas USA. Water points, supplemental feeding areas and shade patches were delineated within the study site.

Soils in the west part of the ranch were mostly Montell clay (0 to 3% slope) characterized by gently sloping, deep, calcareous soils formed in clayey alluvium on outwash plains (Clay Flat range site; USDA 1976). Soils in the east part of the ranch were mostly undulating Olmos on low ridges characterized by shallow calcareous soils

formed in beds of caliche (Shallow Ridge range site). The ranch was externally fenced and had no natural hydrological sources, but had four water tanks and a large pond on the southeast part of the ranch. There is a network of dirt roads in the ranch to facilitate cattle and deer management. The property was under a continuous year-long grazing schedule with a stocking rate of 15 ha/AU. Supplemental feed operations occurred year-round, but with higher frequency during the non-growing winter season at least three times per week between 10:00 and 15:00 at one location per operation (Fig. 4.1). The supplement consisted in 20% (crude protein) breeder range cubes, which is a feed for mature beef cattle on pasture.

The study area had a 29.4% woody cover composed by low-growing, thorny vegetation that formed dense mottes of small trees and shrubs with a grass matrix. Small trees of live oak, (*Quercus virginiana*), formed mottes scatted throughout the landscape which provided shade and these are surrounded by a diverse variety of shrubs. The dominant shrubs inside the ranch were catclaw acacia (*Acacia greggii*), guajillo (*Acacia berlandieri*), Texas persimmon (*Diospyros texana*), agarita (*Mahonia trifoliate*), whitebrush (*Aloysia gratissima*), hogplum (*Colubrina texensis*), guayacan (*Guaiacum angustifolium*), honey mesquite (*Prosopis glandulosa*), twisted acacia (*Acacia schaffneri*), spiny hackberry (*Celtis ehrenbergiana*), and cenizo (*Leucophyllum frutescens*). Succulents like Texas pricklypear (*Opuntia engelmannii*), tasajillo (*Opuntia leptocaulis*), and Yucca spp. are also common. Herbaceous species are mostly composed of Halls panicum, *Panicum hallii* var. *hallii,* hairy tridens (*Erioneuron pilosum*), common curlymesquite (*Hilaria belangeri*), Texas grama (*Bouteloua rigidiseta*), sideoats grama (*Bouteloua curtipendula* var. *curtipendula*), threeawn sp. (*Aristida* spp.), plains bristlegrass (*Setaria leucopila*), slim tridens (*Triden muticus* var. *muticus*), red grama (*Bouteloua trifida*), and Texas wintergrass (*Nassella leucotricha*). Common forbs include cardinal feather (*Acalypha radians*), Indian mallow (*Abutilon fruticosum*), orange zexmenia (*Wedelia texana*), frostweed (*Verbesina virginica*), ruellia (*Ruellia metzae*), ragweed (*Hymenopappus artemisiifolius* var. *artemisiifoliu,)*, silverleaf nightshade (*Solanum elaeagnifolium*), hairy tubetongue (*Justicia pilosella*), cedar sedge

(*Carex planostachys*), and prostrate lawnflower (*Calyptocarpus vialis*) (R. Cooper personal observation; TAMU Uvalde Herbarium, 2008).

Animal selection and GPS collars

Collars containing GPS receivers (Lotek GPS 3300LR; Lotek Engineering, Newmarket, Ontario, Canada) were placed on 11 randomly selected individuals from a single herd of 31 free-ranging Bonsmara cows (*Bos taurus*). The animals were four to six years old during the study period and had an average weight of 1193.2±38.4 kg during the study period. The herd has been in the study site since birth. The 11 selected individuals and their respective GPS collars were kept constant throughout the study. Animals were handled according to Texas A&M University System approved animal use protocols (AUP 2007-167).

Sampling period and data processing

The GPS collars provided information on location, date, time, ambient temperature, and animal activity on two axes. Location was accurate to within 2m after differential correction (Lotek 2006). The wide range temperature transducer measured and recorded ambient temperature with accuracy of ± 1°C within the operating temperature of the collar. We used the average temperature from all collars to obtain diurnal and seasonal ambient temperatures.

Spatial data with successive records separated by short time intervals and the non-random movement of animals can produce autocorrelated points with redundant information that violates statistical independence (Swihart & Slade 1997; de Solla et al. 1999). Preliminary analyses (Perotto-Baldivieso et al. In press) indicate that 120 minutes intervals between GPS fixes can significantly reduce autocorrelation. Therefore, we used a GPS fix interval of 120 minutes for the seasonal analysis. Positional and activity data was recorded at synchronized fix intervals for all 11 individuals for 21 days per trial. To account for within season variability, two sampling trials per season (i.e. autumn, winter, spring, summer) were conducted for a total of 8 trials from September 2007 to August

2008. At the end of each period data was retrieved from the collars and it was differentially corrected using N4 v.1.2138 Differential post-processing software (Lotek 2006; Base Station Del Rio, TX; NOAA 2007). When differential corrections were not possible, an uncorrected position was used (Ganskopp & Johnson 2007). When no collar integration was obtained, series of three consecutive records were interpolated to complete the data set. If more than three successive fixes was not obtained, that portion of the dataset was omitted from analyses.

Four periods of the day were selected to capture the diurnal variation in animal behavior based on past research (Gary et al. 1967; Stricklin et al. 1976; Scoones 1995; Ganskopp 2001; Parsons et al. 2003). The periods were: (1) early morning (grazing bout): first three hours after sunrise; (2) midday (resting bout): three hours between the solar noon; (3) late afternoon (grazing bout): last three hours before sunset; and (4) midnight (resting bout): three hours between time opposite of solar noon. Data was processed using ArcView 3.2 and ArcMap 9.3 (ESRI, Redlands, CA) to convert the differentially corrected data (latitude/longitude form) to Universal Transverse Mercator (UTM 14-N) coordinate system to allow the algebraic derivation of straight-line distances between successive GPS fixes (Ungar et al. 2005).

Estimation of available forage biomass using NDVI

We estimated and compared the Normalized Difference Vegetation Index (NDVI) as an indicator of seasonal changes in the amount of forage biomass. For each season we acquired one Landsat 7 ETM+ scene (Path 28, Row 40) from the U.S. Geological Survey (USGS 2010): Earth Resources Observation and Science Center (EROS). Landsat scenes have a spatial resolution of 30 m for bands 1 through 5 and 7 and a temporal resolution of 16 days. For this study we focused our analyses on bands 3 and 4 (red and near infrared). Since cattle herd GPS data collection was conducted from September 2007 to August 2008, for autumn we used a Landsat scene from November 2nd, 2007 with 0% cloud cover. For winter, we used a scene from February 6th, 2008 with 0% cloud cover. For spring, we used a scene from April 10th, 2008 with 7% cloud cover.

Finally, for summer we used a scene from July 15th, 2008 with 0% cloud cover. Downloaded scenes were already processed to Standard Terrain Correction (Level 1T) which provides systematic radiometric and geometric accuracy by incorporating ground control points while employing a Digital Elevation Model (DEM) for topographic accuracy (USGS 2010). Once the scenes were decompressed we used the software ENVI v.4**.7** (ITT Visual Information Solutions, Boulder, CO) for processing and analysis of the geospatial imagery.

Due to the fact that, during remote sensing, solar radiation passes through the atmosphere before it is collected by the sensor, the images include information about the atmosphere and the earth's surface (Atmospheric correction module v. 4.7; ITT 2009). To accurately analyze surface reflectance, it is important to remove the influence of the atmosphere (e.g. scattering and absorption) during pre-processing (Jensen 2005). Atmospheric properties such as amount of water vapor, distribution of aerosols, and scene visibility must be taken into account through inference from their imprint on hyperspectral radiance data. These properties are then used to constrain accurate models of atmospheric radiation transfer to produce an estimate of the true surface reflectance. Atmospheric correction is particularly necessary for measurements of biophysical parameters (e.g. biomass), especially for comparisons over time such as this study (Jensen 2005). Moreover, the contribution from the atmosphere to NDVI can amount more than 50%, so it is essential to remove this deleterious effect before further analysis. For this study, we used the atmospheric correction modeling tool for retrieving spectral reflectance from multispectral radiance images: Fast Line-of-sight Atmospheric Analysis of Spectral Hypercubes (FLAASH) developed by Spectral Sciences, Inc.. The FLAASH extension in ENVI is a first-principles atmospheric correction tool that corrects wavelengths in the visible through near-infrared and shortwave infrared regions, up to 3 μm that incorporates the MODTRAN4 radiation transfer code and computes a unique solution for each image.

To meet the input requirements for FLAASH, we first used the ENVI Landsat Calibration and Band Math tools to calibrate the image into radiance units of

$\mu W/cm^2*nm*sr$. Then we used the Layer Stacking tool to have all the bands as one layer and used the Convert Data tool to convert the layer into band interleaved by line format (BIL). Since the input image is already correctly scaled we used a single scale factor for all bands. Latitude, longitude, sensor type, flight date and flight time was specified for each image using the metadata file provided with the scenes. For the atmospheric model we will use "Mid-Latitude Summer" and Mid-Latitude Winter" (Table 4.1). We also used the Kaufman-Tanre aerosol retrieval which estimates a scene average visibility using the dark pixel reflectance ratio method.

Table 4.1. Column water vapor amounts and surface temperatures for the MODTRAN model atmospheres

Model atmosphere	Water vapor (std atm-cm)	Water vapor (g/cm^2)	Surface air temperature (^oC)
Mid-latitude summer (MLS)	3636	2.92	21
Mid-latitude winter (MLW)	1060	0.85	-1

Lastly, after each image was atmospherically corrected we calculated NDVI using ENVI. We also calculated NDVI on the images before they are atmospherically corrected to compare results and assess the influence of atmospheric correction on NDVI values and patterns. Mean comparisons were conducted to examine the overall seasonal patterns NDVI changes as an indicator of seasonal forage biomass fluctuations. One-way analysis of variance Test (F; $\alpha = 0.05$) was used to examine statistical differences between NDVI results of both original and atmospherically corrected images for each season.

Analysis of shade patches and water and supplemental feed areas

Shade patches were delineated using a two-meter resolution 2006 aerial photograph (Texas Natural Resources Information System, 2008) and ArcMap 9.3 to

create a shade polygon vector layer of tree patches (Fig. 4.1). A ten meter buffer was created around all shade patches to compensate for GPS fix error and shade extent beyond the patch edge. Location of water and feeders were plotted with a sub-meter accuracy GPS unit (Trimble GeoXT, Sunnyvale, CA). We defined use as the percent number of GPS fixes per day per trial that fell within the specified selection criteria. A 30 meter buffer was created around water and supplemental feeding points. The 30 meter buffer was selected based on locational error of GPS instruments, size of the herd, field observations (estimated spread of the group during feeding and watering events) and to avoid, as much as possible, overlap among features (Cooper et al. 2010). X and Y data from the GPS collars was added and exported to create a layer of all the GPS fixes for each trial. Data was selected based on the features under analysis and divided into the four time periods and then clipped to obtain only the GPS fixes that fell inside the features using ArcMap 9.3.

Number of GPS fixes per feature, per trial (season) and per period of the day were summarized to estimate the percent and standard error. Mean comparisons were conducted to examine the overall seasonal and diurnal patterns of use. Kruskal-Wallis one-way analysis of variance on ranks Test ($\alpha = 0.05$) was used to examine statistical differences in the percent of GPS fixes per day for shade patches and water and supplemental feeding areas.

Results

Temperature fluctuations and estimation of NDVI

Based on the temperatures collected by the GPS collars, the summer season was the hottest season of the year ($X + SE$ = 30.75+0.07 °C) followed by autumn ($X + SE$ = 25.14+0.12 °C), then spring ($X + SE$ = 23.54+0.16 °C) and finally winter was the coldest season ($X + SE$ = 18.77+0.14 °C). The midday period followed by late afternoon appeared to be the hottest periods of the day for all seasons whereas early morning and midnight were the coldest periods (Table 4.2).

Table 4.2. Mean and standard error of diurnal and seasonal temperatures (°C) collected by the GPS collars

Parameter	Early morning	Midday	Late afternoon	Midnight
Spring				
Mean	19.54	29.08	28.16	17.36
SE	0.18	0.15	0.14	0.16
Summer				
Mean	26.65	35.18	34.77	26.40
SE	0.07	0.08	0.09	0.04
Autumn				
Mean	22.48	30.17	28.42	19.51
SE	0.14	0.08	0.11	0.14
Winter				
Mean	13.28	24.24	24.13	13.43
SE	0.17	0.12	0.12	0.15

Images with NDVI values were produced successfully for both original and atmospherically corrected images (Fig. 4.2). Overall, in the original images, winter and spring appeared with darker pixels whereas summer and autumn appeared with brighter pixels. The atmospherically corrected images had a similar seasonal pattern of pixel brightness, but showed slightly brighter pixels on all images. For the original images, NDVI was significantly lower during the spring and winter seasons and higher during the summer and autumn seasons (F_3,1020 = 35.98, $P < 0.05$; Fig. 4.3). Mean NDVI values for the original images showed small positive or negative values ranging from $X + SE$ = -0.0847+0.0076, N = 256 during the winter season to $X + SE$ = 0.0010±0.0080, N = 256 during the summer season. For the atmospherically corrected images, NDVI was significantly lower but different during the spring and winter season and higher during the summer and autumn seasons (F_3,1020 = 32.40, $P < 0.05$; Fig. 4.3). Mean NDVI values for all the atmospherically corrected images showed larger positive values than

the original images. These values ranged from $X + SE = 0.117+0.0086$, $N = 256$ during the spring season to $X + SE = 0.306+0.016$, $N = 256$ during the autumn season. Even though the atmospherically corrected images showed higher values of NDVI, consequently indicating higher amounts of green vegetation biomass, both the original and the corrected images showed the similar overall seasonal pattern of NDVI. The winter and spring season had the lowest NDVI values and the summer and autumn season had the highest.

The USGS-EROS provides a year-long NDVI estimate for each scene. We obtained their estimate for 2007 and 2008 of the scene that contained our study site to serve as a reference for our results of NDVI. The NDVI values obtained from the entire scene (0.3-0.6) are higher than those obtained from our original and atmospherically corrected images of our study site. However, all three types of images (i.e. original, atmospherically corrected, entire scene) showed the same general seasonal pattern of NDVI where summer and autumn had the highest values and winter had the lowest values.

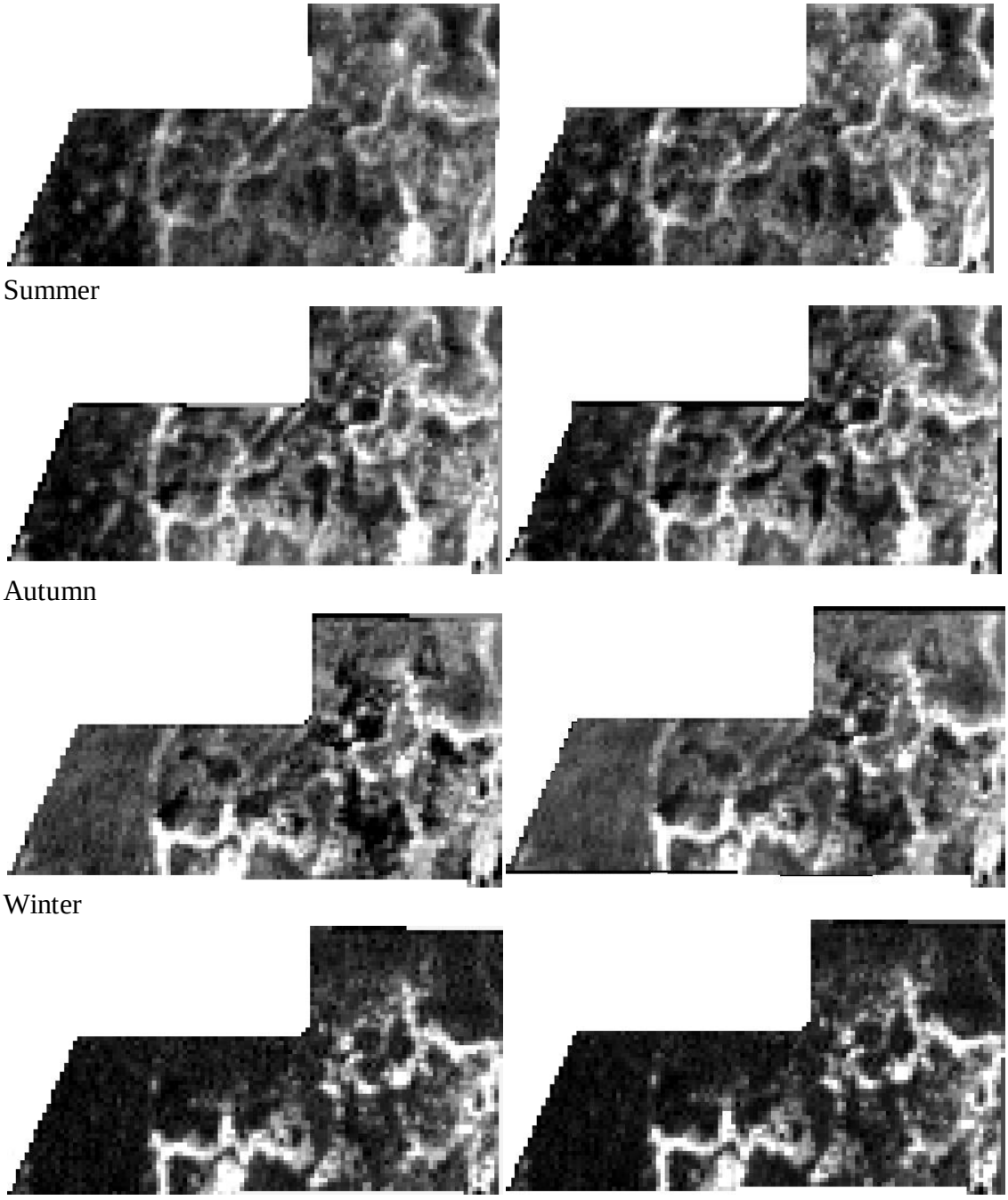


Figure 4.2. Normalized Difference Vegetation Index images produced from four original and four atmospherically corrected images obtained in November 2007 (Autumn), February 2008 (Winter), April 2008 (Spring), and July 2008 (Summer) of a 457 ha semi-arid rangeland in South Texas, USA.

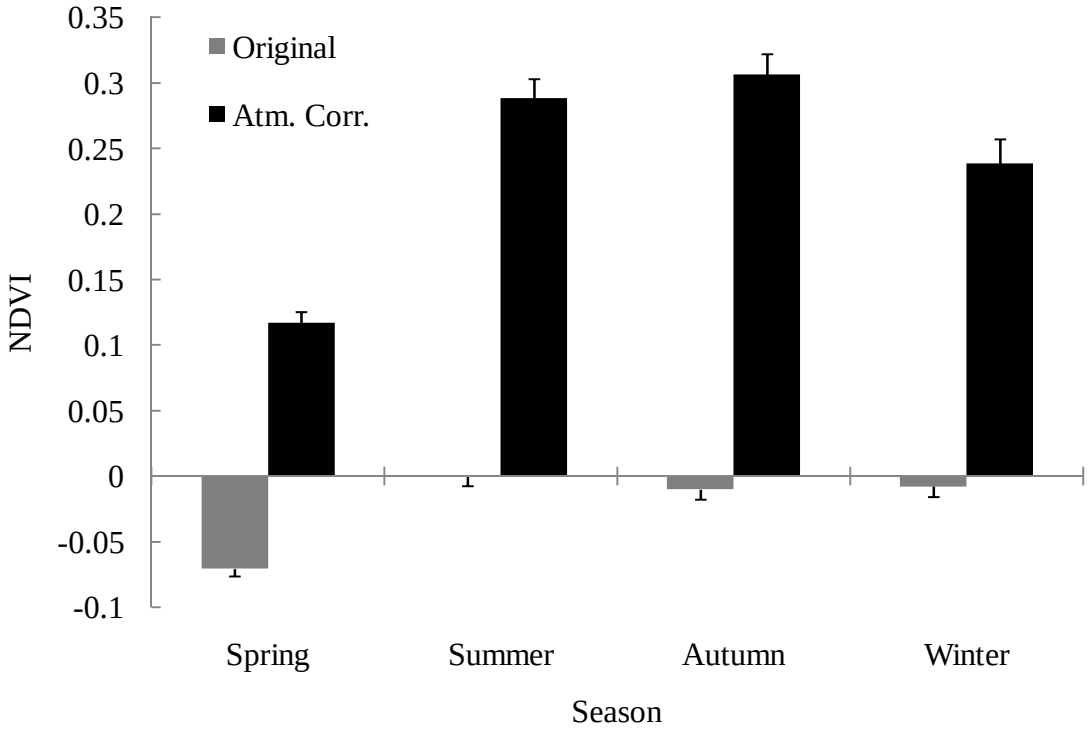


Figure 4.3. Mean NDVI (±SE) of four original and four atmospherically corrected images obtained on November 2007 (Autumn), February 2008 (Winter), April 2008 (Spring), and July 2008 (Summer) of a 457 ha semi-arid rangeland in South Texas, USA.

Seasonal and diurnal use of shade patches by cattle: Quantifying GPS fixes

When we compared the percent of GPS fixes in shade patches per day between each season we found that the lowest percent occurred during the spring ($X + SE$ = 24.61+1.18 %, N = 43) and summer seasons ($X + SE$ = 23.64+1.20 %, N = 42) and higher during the autumn ($X + SE$ = 31.59+1.36 %, N = 35) and winter ($X + SE$ = 34.55+1.14 %, N = 42) seasons (H_3 = 18.98, $P < 0.05$; Fig. 4.4). In terms of periods of the day, with all seasons combined, we found that the midday period ($X + SE$ = 13.27+0.66 %, N = 162) had the highest percent of GPS fixes per day in shade patches followed by the early morning period ($X + SE$ = 8.17+0.49 %, N = 162) and then by the late afternoon period ($X + SE$ = 6.48+0.45 %, N = 162) and the midnight period ($X + SE$ = 6.24+0.55 %, N =

162) which both had significantly the lowest percent of GPS fixes ($H_3 = 121.70$, $P < 0.05$; Fig. 4.5). A more in depth analysis reveals that some differences exist among time periods within each season ($H_{15} = 167.72$, $P < 0.05$; Fig. 4.6). Specifically, during the spring season the early morning ($X + SE = 10.62+1.00$ %, $N = 43$) and midday periods ($X + SE = 15.24+1.26$ %, $N = 43$) had a significantly higher percent of GPS fixes per day in shade patches than during the late afternoon ($X + SE = 5.51+0.79$ %, $N = 43$) and midnight periods ($X + SE = 5.35+0.94$ %, $N = 43$). The summer season exhibited a similar pattern where the midday period ($X + SE = 17.41+1.31$ %, $N = 42$) had the highest percent of GPS fixes per day followed by the early morning period ($X + SE = 10.70+0.96$ %, $N = 42$) and then the late afternoon ($X + SE = 5.72+0.59$ %, $N = 42$) and midnight periods ($X + SE = 4.13+0.48$ %, $N = 42$) having the lowest number of fixes. On the other hand, the percent of GPS fixes per day for the time periods during the autumn season did not differed significantly among each other ($X + SE = 11.93+1.27$ %, $N = 35$). The winter season did showed significant differences among time periods but exhibited a slightly different pattern than the spring and summer season where the midday ($X + SE = 16.84+1.34$ %, $N = 42$) followed by the midnight ($X + SE = 10.92+1.14$ %, $N = 42$) period had the highest percent of GPS fixes per day in shade patches whereas the early morning ($X + SE = 8.49+0.73$ %, $N = 42$) and late afternoon ($X + SE = 10.00+0.84$ %, $N = 42$) had the lowest. Another notable difference occurred among the same time periods between seasons where the average number of GPS fixes per day in shade patches during the late afternoon was significantly lower during spring and summer and higher during the winter season. We also found a significantly higher use of shade patches at midnight during the winter season than during the summer season.

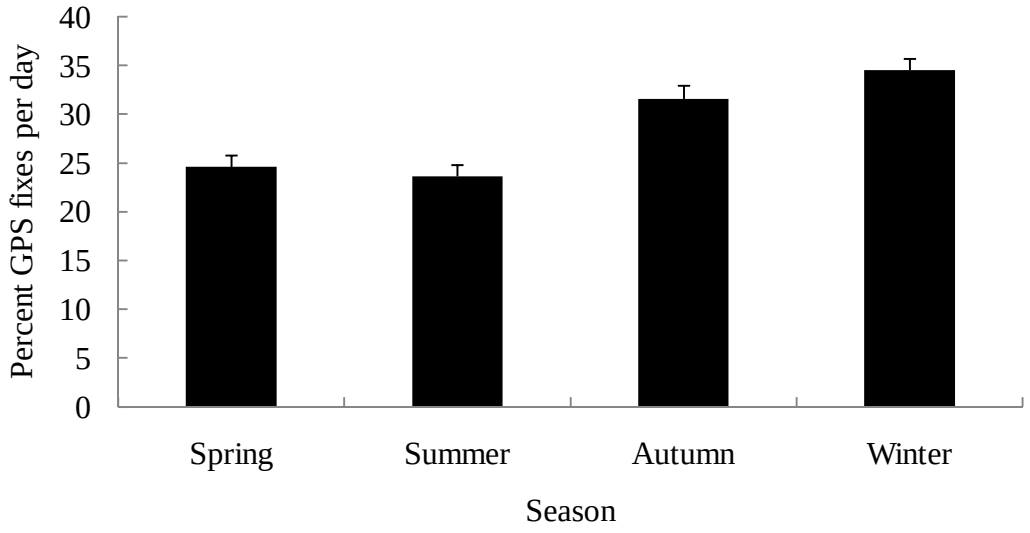


Figure 4.4. Percent and standard error of GPS fixes inside shade patches per day of a free-ranging cattle herd (N = 11) for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

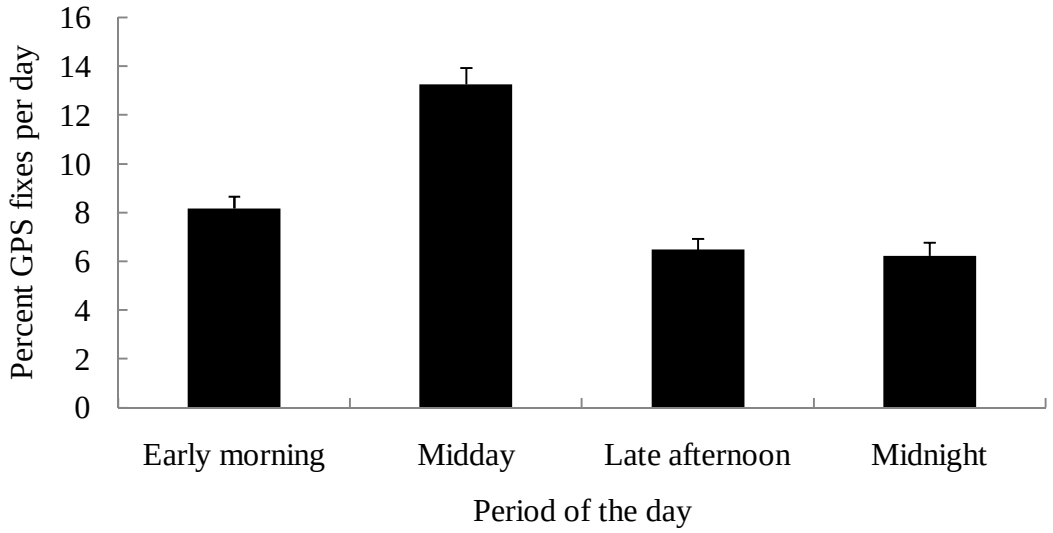


Figure 4.5. Percent and standard error of GPS fixes inside shade patches per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

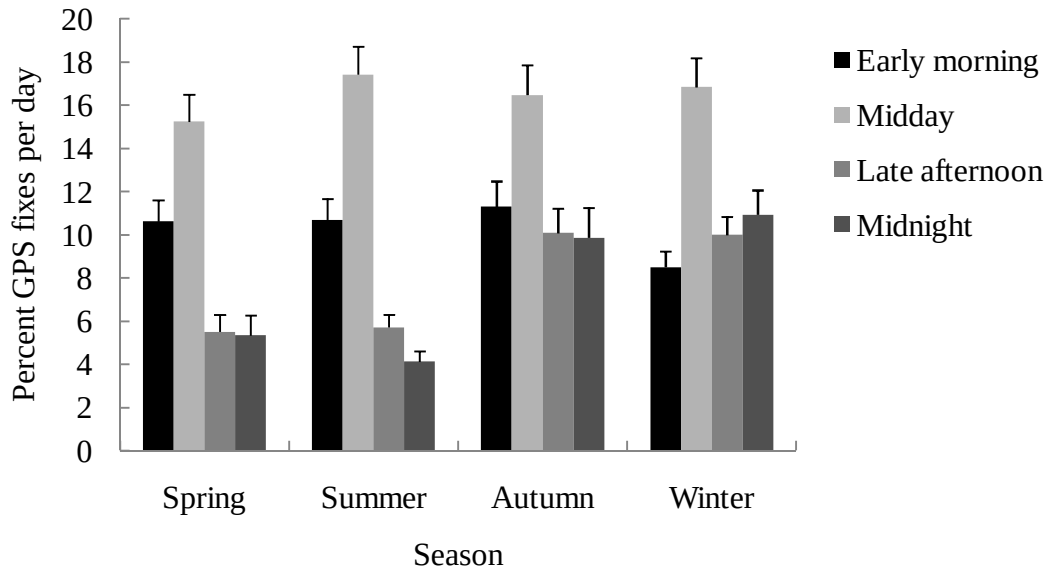


Figure 4.6. Percent and standard error of the number of GPS fixes inside shade patches per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

Seasonal and diurnal use of water areas: Quantifying GPS fixes

The percent of GPS fixes per day 30m around water points was highest during the winter season and lowest during autumn, but this pattern was not significant between seasons when all time periods were combined ($X + SE$ = 9.67+0.70 %, N = 33; Fig. 4.7). However, when all seasons were combined the midday period ($X + SE$ = 5.46+0.50 %, N = 130; Fig. 4.8) showed the highest percent of GPS fixes per day 30m around water points which was followed by the early morning ($X + SE$ = 2.52+0.32 %, N = 130) and late afternoon ($X + SE$ = 1.68+0.21 %, N = 130) time periods and the midnight period ($X + SE$ = 0.09+0.04 %, N = 130) had the lowest (H_3 = 244.25, $P < 0.05$). A detailed analysis of the time periods within each season showed that there were significant differences among some time periods for all seasons (H_{15} = 257.14, $P < 0.05$; Fig. 4.9). During the spring season, the highest percent of GPS fixes per day was found during the midday ($X + SE$ = 4.84+0.75 %, N = 34) and early morning ($X + SE$ = 3.23+0.73 %, N = 34) hours followed by late afternoon ($X + SE$ = 1.36+0.36 %, N = 34) and midnight

period had the lowest (*X* +*SE* = 0.11+0.07 %, *N* = 34). The summer period exhibited the exact same pattern with the midday period (*X* +*SE* = 5.26+1.00 %, *N* = 35) having the largest average number of GPS fixes 30m around water points per day and the midnight period (*X* +*SE* = 0.21+0.13 %, *N* = 35) having the lowest with early morning (2.36%±0.52, *N* = 35) and late afternoon (*X* +*SE* = 0.96+0.18 %, *N* = 35) falling in between. The autumn season presented a different pattern than spring and summer in which the midday, late afternoon and early morning periods had significantly similar average number of GPS fixes per day 30m around water points (*X* +*SE* = 2.67+0.73 %, *N* = 27). However, the midnight period (*X* +*SE* = 0.03+0.02 %, *N* = 27) was significantly lower. Lastly, the winter season had a pattern similar to the spring and summer seasons except that there was a shift between early morning and late afternoon. Here, the midday (*X* +*SE* = 7.38+1.14 %, *N* = 34) and late afternoon periods (*X* +*SE* = 2.71+0.59 %, *N* = 34) had the highest average number of GPS fixes per day 30m around water points which was then followed by the early morning period (*X* +*SE* = 2.26+0.59 %, *N* = 34) and no observations were found during the midnight period (0, *N* = 34).

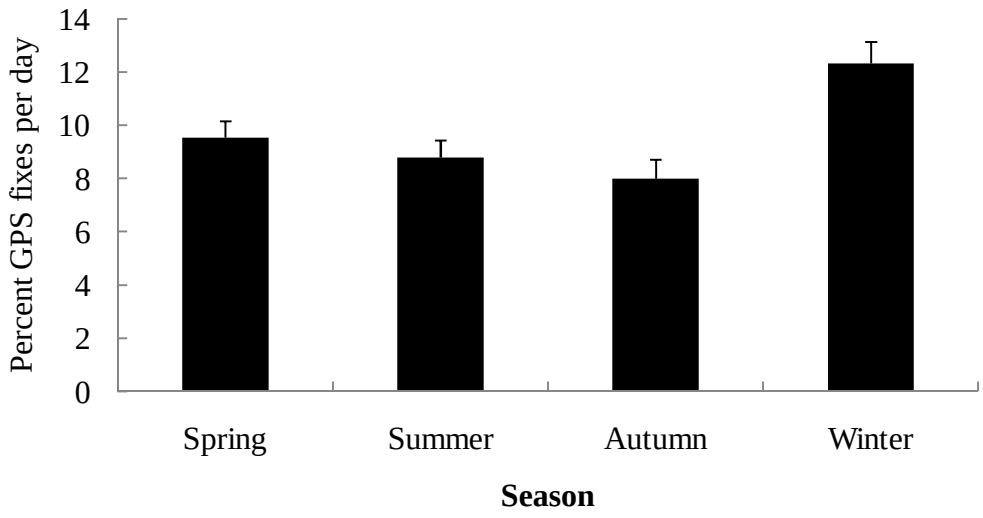


Figure 4.7. Percent and standard error of GPS fixes 30m around water points per day of a free-ranging cattle herd (N = 11) for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

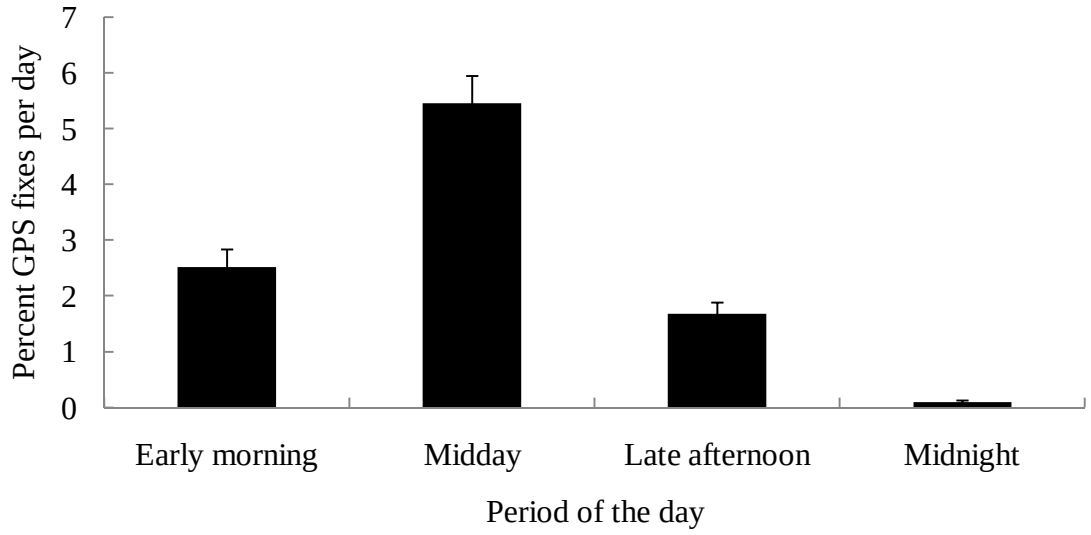


Figure 4.8. Percent and standard error of GPS fixes 30m around water points per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

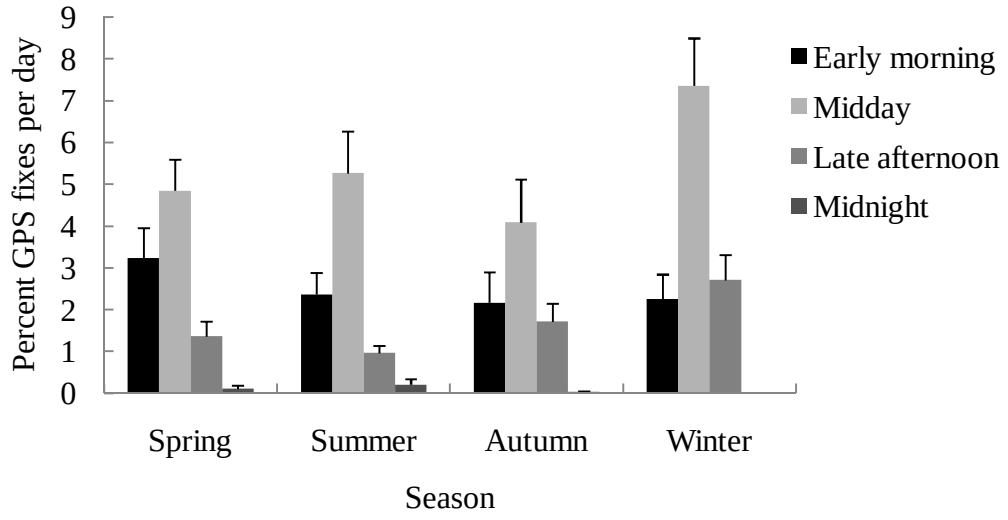


Figure 4.9. Percent and standard error of the number of GPS fixes 30m around water points per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

Seasonal and diurnal use of supplemental feeding areas: Quantifying GPS fixes

Cattle were feed three times per week during late morning or early afternoon at one location per operation. Partially similar to the overall seasonal pattern for use of water areas, the winter season had the highest percent GPS fixes per day 30m around feeding areas and autumn had the lowest, but it was not significant between seasons ($X +SE$ = 11.80+0.78 %, N = 33; Fig. 4.10). In terms of periods of the day, with all seasons combined, we found the same pattern as the one observed for the water areas where the midday period ($X +SE$ = 7.60+0.51 %, N = 133; Fig. 4.11) showed the highest percent of GPS fixes per day 30m around feeding points which was followed by the early morning ($X +SE$ = 2.60+0.30 %, N = 133) and late afternoon ($X +SE$ = 1.95+0.24 %, N = 133) time periods and the midnight period ($X +SE$ = 0.49+0.13 %, N = 133) had the lowest (H_3 = 216.33, $P < 0.05$). There were also differences among time periods within each season (H_{15} = 239.97, $P < 0.05$; Fig. 4.12). Similar to the pattern observed around water areas, during the spring season the highest percent of GPS fixes per day around supplemental feeding areas was found during the midday ($X +SE$ = 8.16+0.85 %, N = 36; Fig. 4.12) period and followed by early morning ($X +SE$ = 3.34+0.67%, N = 36) and late afternoon ($X +SE$ = 1.85+0.37 %, N = 36) and the midnight period had the lowest ($X +SE$ = 0.46+0.16 %, N = 36). The summer period exhibited a different pattern with the midday period ($X +SE$ = 8.18+0.93 %, N = 35) being the only different period having the largest percent of GPS fixes 30m around supplemental feeding areas per day and the rest of the time periods having similar values ($X +SE$ = 1.56+038 %, N = 35). During the autumn season we found the same pattern observed around water points where midday, late afternoon and early morning periods had significantly similar percent of GPS fixes per day 30m around supplemental feeding areas ($X +SE$ = 3.49+0.74 %, N = 26) and the midnight period ($X +SE$ = 0.08+0.03 %, N = 26) being lower. Lastly, the winter season had a pattern similar to the spring season. The midday ($X +SE$ = 9.52+1.15 %, N = 36) and late afternoon periods ($X +SE$ = 3.97+0.71 %, N = 36) had the highest percent of GPS fixes per day 30m around supplemental feeding areas which was then followed by the early morning period ($X +SE$ = 2.10+0.44 %, N = 36) and, finally, midnight showed

the lowest value ($X + SE$ = 0.04+0.03 %, N = 36). Other notable difference occurred among the same time period between seasons where the average number of GPS fixes per day in 30m around supplemental feeding areas during the late afternoon was lower during summer and higher during the winter season. Also, during the midnight period the average number of GPS fixes around supplemental feeding areas was lower during the winter season and higher during the spring and summer seasons.

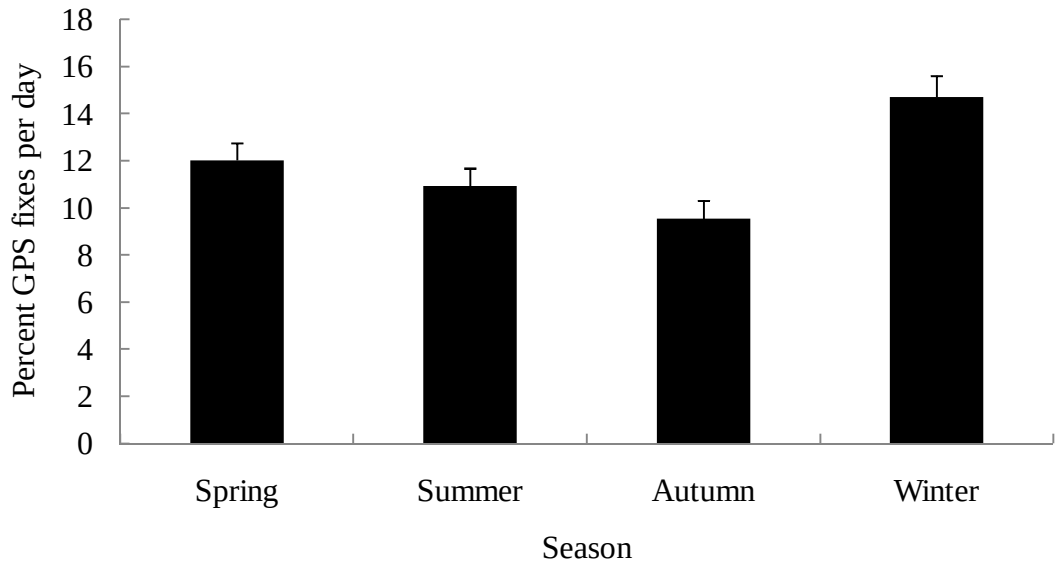


Figure 4.10. Percent and standard error of GPS fixes 30m around supplemental feed points per day of a free-ranging cattle herd (N = 11) for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

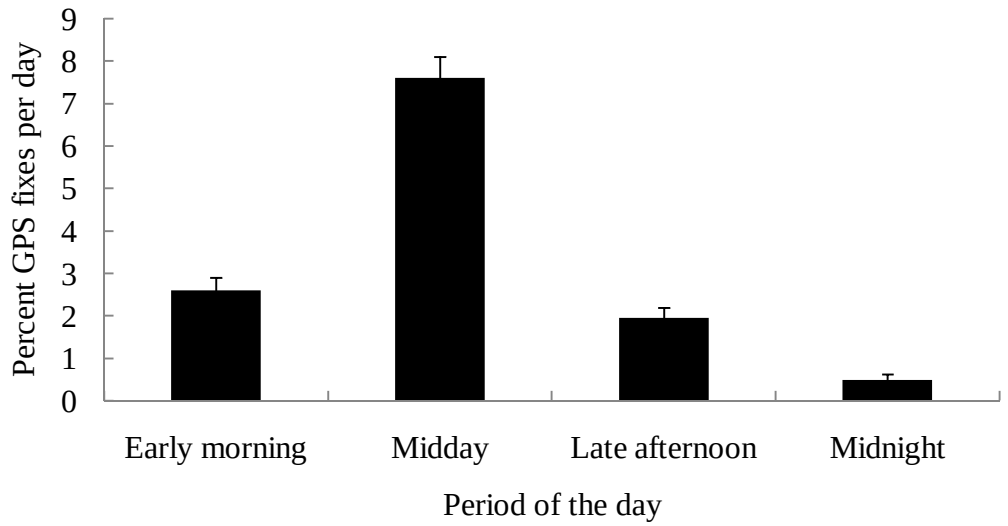


Figure 4.11. Percent and standard error of GPS fixes 30m around supplemental feed points per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA. Supplemental feeding occurred around midday 3-4 times per week at a single location.

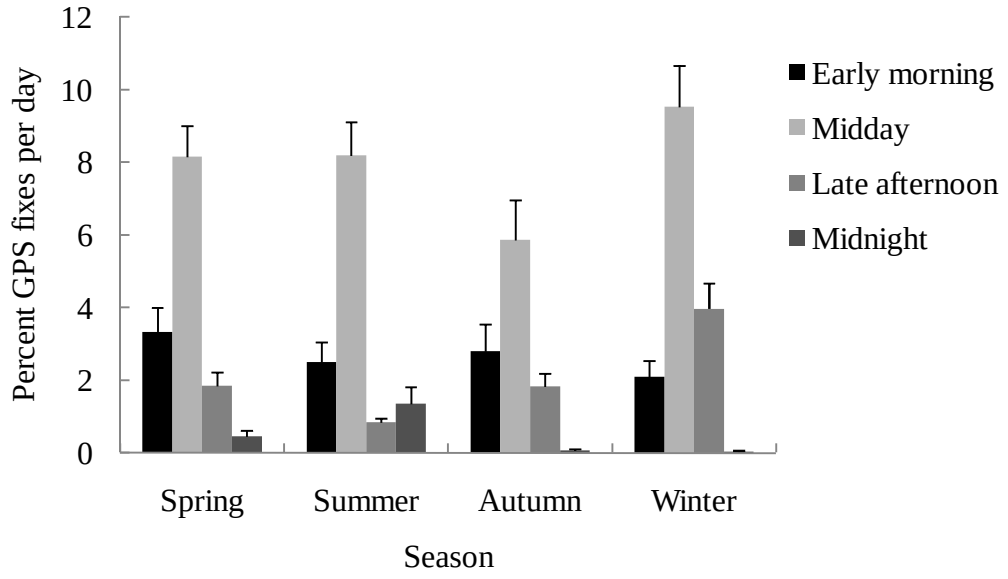


Figure 4.12. Percent and standard error of the number of GPS fixes 30m around supplemental feed points per day of a free-ranging cattle herd (N = 11) during four 3-hour time periods for eight trials of three weeks from September 2007 to August 2008 in a semi-arid rangeland in South Texas, USA.

Discussion

The use of multiple temporal scales (seasonal and diurnal) allowed us to uncover how scale-dependent processes, resources and landscape features interact and influence ungulate herd spatial distribution in a shrub-dominated savanna. Although abiotic factors such as slope and distance to water are usually regarded as the primary determinants of grazing distribution patterns in ungulates, other microsite characteristics seem to be playing a higher influential role than previously acknowledged (Senft et al. 1987). The interaction between seasonal and diurnal temperature fluctuations and shade patch availability seems to be exerting a high significant force when water and supplemental feed are not limiting. The use of shade patches was influenced by seasonal changes in forage biomass and seasonal and diurnal fluctuations in temperature. The information obtained in this study increases our knowledge of the scale-specific responses of animals to the environment and under which a herds function and perceive the landscape (Bailey et al. 1996; Johnson et al. 2002; Butt 2010). Overall, we found expected and unexpected patterns in the use of shade patches, water sources and areas with concentrated feed as a function of the season and associated available forage biomass and time of the day. Our results showed some differences in the use of shade patches and areas with concentrated feed among seasons for the same time period suggesting that a cross-scale interaction between processes occurring at two temporal scales is affecting the behavior of the herd. To our knowledge, this study is the first one to consider the explicit spatio-temporal dynamics of a large herbivore herd in relation to specific landscape attributes using multiple temporal scales in a level terrain brushy savanna environment.

NDVI as indicator of available forage biomass

Seasonal variations in available forage biomass was successfully captured using NDVI, but atmospheric correction of original images must be carefully performed to obtain more accurate estimates of surface reflectance used for calculation of vegetation indices. The first objective was to estimate and compare seasonal NDVI as an indicator of available forage biomass to explore its relationship to cattle herd movement dynamics

in the context of shade, water and supplemental feed use. Although, the NDVI values of the original images were significantly lower than the values of atmospherically corrected images, they both showed the same overall pattern in NDVI seasonal fluctuations. Spring and winter had the lowest values and summer and autumn had the highest. Our results also showed that atmospherically corrected images resulted in higher brightness values more representative of the surface reflectance. We were able to reduce atmospheric attenuation (i.e. path radiance) and thus obtained higher and more accurate (closer to the ground measurement) NDVI values (Jensen 2005). Having accurate NDVI values is important because we can monitor seasonal and inter-annual changes in vegetation growth and activity. However, it is necessary to mention that because NDVI is a nonlinear ratio-based index it can be influenced by additive noise (e.g. atmospheric path radiance), it also exhibits scaling problems with saturated signals in high-biomass conditions, and finally it is very sensitive to canopy background variations. Nonetheless, NDVI is also advantageous because the rationing reduces many forms of multiplicative noise from multiple bands of multiple-date imagery and has been successfully used to increase our knowledge of the spatial and temporal variability of vegetation resources in savanna ecosystems for at least three decades (Jensen 2005; Butt 2010).

Previous studies conducted in the same area with the same group of animals demonstrated that the cattle herd had a higher dispersion during the summer and autumn season and lower dispersion during spring and winter (Chapter 2). Hence, here as in other studies, the spread pattern seems to be explained, in part, by seasonal changes in available forage biomass, causing dispersive movement to explore larger grazing areas and subgroup division (Sato 1982). However, this dispersive grazing movement seems to be significantly reduced during the non-growing dry season possibly due to low forage biomass and congregation of subgroups in certain areas of the pasture. The subsequent objectives allowed us to assess whether the measured use of some distinct landscape attributes, such as shade patches, water and supplemental feed areas, could help explain the seasonal distribution patterns of the herd.

Seasonal and diurnal use of shade patches

The use of shade patches is a function of animal response to the interaction between seasonal and diurnal fluctuations in temperature, nutritional requirements and thermoregulatory actions. The second objective was to assess the relationship between the use of shade patches by the cattle and seasonal changes in available biomass and diurnal fluctuations in temperature. We found that the average number of GPS fixes per day in shade patches was significantly lower during the spring and summer seasons and higher during the autumn and winter seasons. Thus, shade patches are being more used by cattle during the autumn and winter seasons and less during the spring and summer seasons. This is an unexpected result because previous studies have reported that during the summer, the cows spend a larger amount of time under shade trees near water or aggregated to avoid flies and during winter they spend most of the time at warmer exposures and avoided shade trees in a pasture in the dry tropics of Rockhampton, Queensland and experimental pastures in Japan (Sato 1982; Harris et al. 2002). On two earlier studies of cattle spatio-temporal dynamics conducted with the same group of animals in the same study site, we found that during the winter season, the herd had a significantly smaller spread and members spent more time closer to each other, thus behaving in a more aggregated spatial pattern than during the growing summer season where members were more spread from each other (Chapter 2). This overall aggregation during the winter season might then be explained, in part, by congregation of animals in shade patches although we expected this type of physiological response to occur during the hotter temperatures of the summer. However shade affects more than just the cattle, typically shade is provided by trees which occur on slightly deeper soils. Differences in soils and the effect of shading will reduce moisture loss from soils and vegetation and thus it is likely that there is more edible forage remaining in shaded areas through the non-growing season.

On a diurnal basis we found that, overall, the midday period had the highest mean temperature. At this time we recorded the highest number of GPS fixes per day in shade patches followed by the early morning period and then by the late afternoon

period and the midnight period. This evidence agrees with many other studies that have shown that on a diurnal scale, large herbivores congregate in shade areas during the hottest periods of the day. This behavior is, in part, explained by thermoregulatory actions, where the animals rest in compact groups under shade trees to lose heat and regulate body temperature (Sato 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; DelCurto et al. 2000; Parsons et al. 2003; Harris et al. 2002, 2007; Cooper et al. 2008). These results are further supported by our previous study in which we found that, throughout the year, herd spread was significantly lower during midday relative to the other three time periods (early morning, late afternoon, and midnight) (Chapter 2). However, the large use of shade patches during early morning was unexpected because this time period, together with late afternoon, is usually associated with grazing activities which occur in open pastures (Gary et al. 1967; Stricklin et al. 1976; Scoones 1995; Ganskopp 2001; Parsons et al. 2003). We would have expected a higher relative use of shade patches during the midnight period which is associated with the resting/sleeping activity, not for the shade but as sites cattle habitually rest in. However, when we compare the midnight period across seasons, winter had a significantly higher use of shade patches by cattle than the summer season. This behavioral pattern might be explained by two mechanisms that have been observed in the field and in other studies. The higher use of shade patches during winter might be due to cold wind avoidance mechanisms and the lower use of shade patches during the hotter summer season could be due to compensatory night-time feeding and energy conservation strategies in open pastures (Bennet et al. 1985; Scoones 1995). These mechanisms are also supported by the patterns observed during late afternoon where the use of shade patches was significantly lower during spring and summer and higher during the winter season. Here again animals might be using the open areas of the pasture at this time during spring and summer driven by moderate temperatures and in the winter avoiding cold winds in shaded/sheltered areas (Sato 1982). The autumn season did not show a clear pattern of shade patch use among time periods, as the animals transitioned to the winter pattern when the midday period still had the highest average number of GPS fixes per day in

shade patches, but it was followed by midnight and late afternoon and the lowest use of shade patches occurred during early morning. Hence, besides the governing influence of shade patches during midday on the spatial distribution of cattle throughout most of the year, in winter these patches seem to be a focus for animals during night-time.

Seasonal and diurnal use of water and supplemental feed areas

Although water and, to a certain extent, feeding areas are known to greatly influence ungulate movement patterns it seems that their effects can be overshadowed by the influence of shade patches when water or feed are not limiting. The third objective was to explore the seasonal and diurnal influence of water and supplemental feeding points on cattle distribution patterns. On a seasonal basis, there was no overall significant pattern of use of water and supplemental feed areas when all time periods were combined. The placement of supplemental feed and water occurred year-round, but given the low forage production characteristic of the dry winter season, we expected cattle to be more responsive and have a higher frequency of use during the winter supplements and water to meet energetic demands (Sato 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; DelCurto et al. 2000; Parsons et al. 2003; Harris et al. 2002, 2007; Cooper et al. 2008). Ungulates such as cattle and caribou tend to congregate in nutrient rich areas which maintain higher quality and availability of herbaceous standing crop than dry land rangeland during the dry non-growing season (Senft et al. 1987; Owens et al. 1991; Johnson et al. 2002). These winter patterns have been found in western rangelands of North America where distribution of cattle during the non-growing season is mostly influenced by supplemental placement of water and feed (Kie & Boroski 1996; DelCurto et al. 2005). However, the aggregation during the winter season observed in our previous and present studies seems to be more related to seasonal fluctuations in shade patch use rather than water and supplemental feed use.

The use of water sources by cattle has been mostly studied at the seasonal scale, but little is known about the diurnal patterns of water use and its relationship to seasonal patterns (Sato 1982; Bennet et al. 1985; Lazo 1994; Coppock et al. 1986; Parsons et al.

2003; Harris et al. 2002; DelCurto et al. 2005; Cooper et al. 2008). On a diurnal basis and with all seasons combined, the animals exhibited the highest use of both water and supplemental feed areas during the midday period followed by late afternoon, early morning and midnight with the lowest amount of use. This pattern correlates with the diurnal fluctuations in temperatures of the periods of time sampled in this study where midday had the highest temperatures, followed by late afternoon, early morning and finally midnight. The higher use of water sources during midday might be related to physiological responses (e.g. osmoregulation) to high temperatures associated to this time period. Also in semi-arid areas tall trees that provide deep shade tend to be restricted to sites with additional water. The low use of these resources at midnight agree with other studies that found that resource use and grazing activity by cattle tend to be minimal during dark hours particularly during the winter season (Gary et al. 1967).

We also found differences in the use of water and supplemental feed areas among some time periods within seasons. During spring, the highest amount of use of both water and supplemental feeding areas occurred during midday followed by late afternoon and early morning and midnight with the lowest values. Evidently, this spring diurnal pattern is the same as the overall pattern observed when all seasons where combined. During summer, the use of water areas was similar to that of the spring, however the use of supplemental feed was slightly different where midday had the highest amount of use but the other three time periods had statistically the same level of use. Moreover, the use of supplemental feeding areas during midnight was significantly higher during the spring and summer seasons and lower during the winter season. Also, the supplemental feeding area use during late afternoon was significantly lower during summer and higher during the winter season. These finding further supports previous evidence that during warmer seasons, animal will shelter more during the day for thermoregulation and exhibit night-time feeding behavior (Bennet et al. 1985; Scoones 1995). The use of water and supplemental feeding areas during autumn was similar for both resources where midday, late afternoon and early morning periods had the same level of use and midnight being significantly lower. Given the moderate temperatures

and the intermediate phase of forage dormancy characteristic of this season, cattle does not seem to have a diurnal differential preference of these resources and, thus present a more evenly distributed resource use (Sato 1982). Lastly, during the winter season animals had a higher degree of use of water and supplemental feeding areas during midday and late afternoon followed by early morning and midnight with the lowest or no observations in the case of water use. Hence, midday seems to be the period of highest use of these resources. However, it is important to acknowledge that feed management might have influenced the diurnal differential use of supplemental feeding areas. Supplemental feed was not constant throughout the entire sampling period rather provided in limited quantities at one location per operation. Feeding activity occurred near the midday period (late morning and early afternoon) at irregular time and day intervals. A noticeable pattern, although not always significant, is that during spring the use of both water and supplemental feeding areas appears to be higher during early morning compared to late afternoon and then this pattern starts to shift as seasons progresses with the use during late afternoon being higher than early morning during winter. This relative shift in seasonal resource use between these two time periods might be related to the interaction between seasonal and diurnal fluctuations in temperature (Scoones 1995). Animals might prefer to use these resources earlier in the day during the warm season to avoid higher temperatures later in the day and during the cold season their strategy shifts to use these resources in the afternoon and take advantage of warmer exposures.

Conclusions

Shade was identified as a major determinant of seasonal and diurnal movement patterns of a cattle herd in semi-arid rangeland. Most previous studies have concluded that forage characteristics, water and slope are the major factors influencing cattle distribution, however this study shows that shade patches can play a major role in affecting the behavior of the herd both at the diurnal and seasonal scale (Lazo 1994; Coppock et al. 1986; Howery et al. 1996; Sowell et al. 1999; DelCurto et al. 2000;

Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Cooper et al. 2008). The differential frequency of use of shade patches is most likely related to changes in forage biomass and temperature fluctuations and physiological and nutritional strategies for thermoregulation and compensatory night-time feeding. The overuse of these shade patches by herds can have negative ecological consequences such as soil compaction and degradation of vegetation surrounding these areas and ultimately affect the productivity of semi-arid ecosystems (Sowell et al. 1999; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Harris et al. 2007; Butt 2010). However, it is shown in this study that the effects of landscape characteristics such as shade patches, vary greatly depending on the scales used to analyze the phenomena. Furthermore, other factors not investigated in this study such as wind direction and roads can also play important roles as influences on cattle herd distribution. As a result, more accurate ethological studies of herd animals depend on our ability to analyze herd dynamics that include the most influential variables using multiple scales to determine how they interact and relate to animal response to the environment.

5. SUMMARY AND CONCLUSIONS

More accurate ethological studies of herd animals depend on our ability to identify and analyze herd dynamics at scales and perspectives that are meaningful to the species of interest. Previous studies have acknowledged that predictive models on ungulate distribution patterns are site-dependent and may not be appropriate for other environments (Bailey et al. 1996) or for species with differing biological requirements. Identifying the scales at which animals function should be a high priority when trying to explain the underlying causes for site selection and resource use by free-ranging animals. The use of GPS technology and spatial recognition software has proven useful to increase our understanding of the complex relationship between social interactions of free-ranging cattle herd, their spatial associations and seasonal and diurnal changes in the environment. We have shown that the use of multiple spatio-temporal scales are necessary to better understand how the environment affects the movement patterns of large herbivores because different processes occur at different scales and influence animal behavior in diverse ways. This type of analysis allowed us to 1) determine the seasonal and diurnal herd spread patterns, 2) describe a methodology that identifies the spatio-temporal parameters that characterize a herd, which is an essential step in exploring the extent and grouping behavior of animals, 3) detect subtle sub-herd formations that might have been imperceptible with other types of analyses (e.g. field observations, VHF telemetry), 4) provide insight as to when the herd is most likely to stay closer together as one unit and, hence, use a smaller area of the pasture and 5) influence of shade patches and water and supplemental feeding areas on the diurnal and seasonal movement patterns of cattle.

Cattle herd spread

Cattle herd spread patterns in semi-arid rangelands are mainly controlled by broad-scale seasonal changes linked to vegetation dynamics. The combined effects of processes operating at different scales, such as seasonal forage production and diurnal

temperature fluctuations, affect cattle dispersive/aggregative movement, thermoregulatory actions, and activity patterns thus strongly influencing their spatial distribution and behavior. The larger herd spread in our study occurred during the warm growing season and the smallest spread during the cold season when forage was less abundant. These results contrast with studies of grazing cattle conducted in northern, mountainous regions and other arid regions where cattle tend to forage and travel in larger and more compact groups during summer when forage is abundant and disperse to search for sparser resources in winter. Furthermore, the combined effect of local environmental conditions such as amount of rainfall, temperature and wind patterns can have a direct impact on how animals behave. Our study site was characterized by very dry conditions with two distinct seasons, growing and non-growing season. These same study organisms would have probably behaved differently if, for example, they were placed in a more tropical and humid region with less temperature and forage biomass fluctuations. The conflicting results of studies on cattle spread patterns between northwestern and southern rangelands in North America highlights the importance of addressing research questions both at fine and broad temporal scales and under different environments in order to understand the basic principals driving behavioral patterns in group-living ungulates. Past research has suggested that seasonal aggregation patterns are, in part, explained by seasonal fluctuations in forage characteristics and type of ecological region where animals congregate near sources of supplemental feed and water during dry and low forage availability periods. However, further investigation showed that the aggregation pattern observed during the non-growing winter season was more related to use of shade/resting patches than use of supplemental feed and water. Diurnal patterns of cattle herd distribution appear to be influenced by the interaction of diurnal fluctuations in temperature and thermoregulatory actions. The herd was significantly more aggregated during the hotter midday period relative to the other three time periods (early morning, late afternoon, and midnight) throughout the year. A more in depth analysis of the influence of seasonality on daily spread shows that the greatest herd spread occurred at different times in the warm and cool seasons. These results

demonstrate that the herd spread at the diurnal scale seemed to be strongly influenced by the overall seasonal pattern. In terms of activity, herd spread was smaller during traveling than during grazing and resting which could be explained by cattle following established trails across the landscape as least effort pathways in a shrub-dominated community that restricts animal movement. Herd spread at different activities varied at different seasons with winter having the smallest spread for all activities than compared to other seasons. These findings further support that a coarse-scale process (i.e. seasonality) is controlling small-scale processes (i.e. diurnal and activity dispersion patterns).

Cattle herd spatio-temporal associations and dominance behavior

Similar to our results of cattle spread, during the non-growing winter season, members of the herd spent more time closer to each other than during the summer growing season when members dispersed. Again, this stronger group aggregation during winter might be driven by seasonal changes in forage availability which affects exploration of unused pastures. Our analysis using coarser spatial scales allowed us to determine the spatial extent of the herd as a function of season. Our analysis using finer spatial scales allowed us to detect subgroup divisions during the summer season. Similar spatio-temporal analysis might allow researchers to understand the natural spacing of individuals within a herd and to identify sub-herd associations to consider when assessing landscape impact of ungulate herds. The contrasting evidence on cattle dispersion and subgroup division patterns found between our study and others conducted in northern and mountainous regions in North America highlight the importance of addressing questions at distinct environments in order to understand ungulate herd behavioral patterns. Contrary to other studies, the herd dispersive pattern and sub-herd grouping dynamics in this flat semi-arid rangeland appears to be mainly controlled by a strong seasonal component and associated forage variation and management regime but not so much a social dominance effect. In sum, this research on herd dynamics incorporated an explicit temporal and spatial analysis that offered baseline information

on herd movement patterns and its approach should prove useful for future herd studies in determining group delineation and identifying fusion-fission patterns.

Landscape influence on cattle herd distribution patterns

This section presented some key findings about the relationship between various seasonal and diurnal processes and landscape characteristics and the spatio-temporal distribution of a cattle herd in a semi-arid rangeland. At the seasonal scale, shade patches were used more by cattle in winter when forage biomass is low season and less during summer when forage biomass is abundant. This indicates that factors other than high temperature were influencing cattle use of shaded areas. However, at the diurnal scale, thermoregulatory actions seem to play a major role in influencing the aggregative movement of animals to shade patches during the midday period, the same vegetation that provides shade at midday was used by cattle as a suitable sheltered resting place at night, particularly in winter. Even though cattle consistently had the highest use of water and supplemental feeding areas in winter there was no significant overall pattern of seasonal changes in the use of these resources. Therefore, the aggregation during the winter season observed in our studies seems to be more related to seasonal fluctuations in shade patch use rather than water and supplemental feed use. On a diurnal basis, cattle used water and supplemental feed the most during midday and the least during midnight for most of the seasons. However, during the summer cattle were more likely to use supplemental feeding areas around midnight and less during late afternoon compared to during winter. This is because in summer cattle tend to be more active at night when daily temperatures fall. Many previous studies have concluded that forage characteristics, water and slope are the major factors influencing cattle distribution, however this study shows that shade patches can play a major role in affecting the spatial distribution of the herd both at the diurnal and seasonal scale (Lazo 1994; Coppock et al. 1986; Howery et al. 1996; Sowell et al. 1999; DelCurto et al. 2000; Turner et al. 2000; Ganskopp 2001; Bailey 2004, 2005; Launchbaugh & Howery 2005; Cooper et al. 2008). The differential frequency of use of shade patches is most likely related to changes in

forage biomass and temperature fluctuations and physiological and nutritional strategies for thermoregulation and compensatory night-time feeding. Based on the spatial distribution patterns presented by the herd throughout the seasons and periods of the day, animals seem to be influenced by an interaction of processes, resources and landscape structures occurring at different spatial and temporal scales such as seasonal fluctuations in available forage biomass, diurnal fluctuations in temperature and the availability and spatial arrangement of shade, water and supplemental feeding areas. Studying these multi-scale interactions are fundamental to more accurately detect the factors that influence animal distribution patterns and develop better predictive models of animal movement dynamics.

Management implications

From a livestock management perspective, inadequately managed grazing systems and poorly understood cattle behavior may lead to severe vegetation degradation due to overgrazing and uneven distribution of pasture use, which may endanger critical species (Butt 2010), change ecological processes (Bailey et al. 1996) and threaten the cattle industry in arid and semi-arid rangelands (Bailey 2004). This study offers baseline information on the movement dynamics of a cattle herd using multiple temporal scales that might be utilized to improve management techniques aimed for a better distributed pasture use that are more compatible with the behavior of the animals. The smaller spread during the dry winter season associated with observed aggregation of individuals in water and supplemental feeding areas in our study could be useful to determine the most critical times to provide supplemental resources and allocate those in areas not frequently used by cattle and thus stimulating the animals to visit unused sites during the non-growing season. Periodical rotations of water/feeding stations could promote the exploration of different areas by livestock thereby reducing the probability of developing a static or fixed spatial memory of predictable preferred sites at the landscape scale. Spatio-temporal analysis of grouping dynamics might allow managers to identify sub-herd associations to consider when assessing appropriate management techniques (e.g.

selective culling, herding) for livestock herds. The problem of aggregation in shade patches by cattle could potentially be improved by an even distribution of shade structures throughout the pasture. Perhaps a more effective, but more labor intensive method is to periodically rotate artificial shade structures to promote the exploration of different areas by livestock. With the use of GPS collar technologies and geospatial management tools, further research in livestock movement dynamics will prove useful for the development and test of management regimes more compatible with the grouping behavior of the herd.

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